Partitioning of foraging habitat resources among bats (Chiroptera) in Great Britain

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Abstract

1. A review of the diets of bats in Great Britain shows that six species eat mainly Lepidoptera, Coleoptera or both. The remaining ten species eat mainly Diptera; *Myotis nattereri* gleans diurnal Diptera, *Rhinolophus hipposideros*, *Myotis mystacinus*, *Myotis brandtii* and *Nyctalus noctula* take Diptera, *Myotis daubentonii*, *Pipistrellus* species and *Nyctalus leisleri* take aquatic Diptera.

2. From broad-band recordings of echolocation calls of bats of known species, a method was developed for species identification. Bats fell into three groups according to call structure. Bats in the first group (*Rhinolophus* species) could be identified unambiguously from calls. Multivariate discriminant analyses on call parameters classified 67% of bats in the second group (*Myotis* species and *Plecotus* species), and 89% of bats in the third group (*Pipistrellus* and *Nyctalus* species and *Eptesicus serotinus*) correctly to species.

3. Foraging activity of bat species, identified as described above, was quantified in ten habitats. Total activity was highest over water. *Myotis* species, *Plecotus auritus* and 45 kHz *Pipistrellus pipistrellus* fed in many habitats; 55 kHz *Pipistrellus pipistrellus* mainly over water; *Nyctalus* species and *Eptesicus serotinus* over pastures and water. Freshwater habitats are important for many species.

4. To reveal how river water quality affects foraging bats, activity and attempted prey captures were measured at paired sites upstream and downstream from sewage outputs. Both were reduced downstream. 45 kHz and 55 kHz *Pipistrellus pipistrellus* were 50% less active downstream than upstream. 45 kHz *Pipistrellus pipistrellus* foraged mainly upstream; *Myotis* species foraged mainly downstream. For the conservation of *Pipistrellus pipistrellus*, water quality may be important; *Myotis daubentonii* may benefit from eutrophication.

5. Conservation measures for endangered bat species should concentrate on specific habitats around roosts. The management of inland waters and conservation of Diptera could benefit many bat species in Great Britain.

"VESPERTILIO the Bat is a paltry animal. It takes its name from the evening (*vesper*).

It has wings, but at the same time it is a quadruped and uses teeth - a thing which one does not usually find in other birds.

The Bat parturates like a quadruped, bringing forth, not eggs, but living young. Moreover, it does not fly with wings, but is supported by a membrane, poised on which just as if on a flight of feathers it moves and weaves about.

There is one other thing about these undistinguished animals, and that is that they hang on to each other alternately, and depend from any place like a cluster of grapes. If the top one let go, they would be all scattered. And this they do from a certain duty of affection, of a kind which it is difficult to find in man."

White, T.H. (ed) (1992) *The Book of Beasts, being a Translation from a Latin Bestiary of the Twelfth Century.* Alan Sutton, Stroud.

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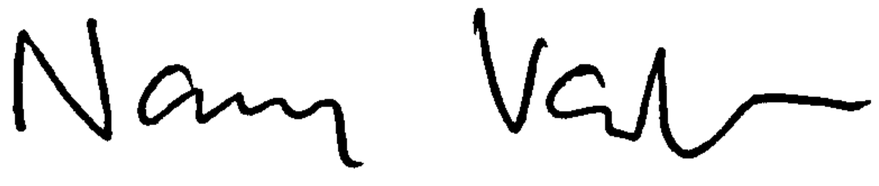
Author's declaration

This thesis and the research described in it are the results of my own original work, except where due acknowledgement has been made. No part of it has been submitted in any previous application for a higher degree.

The views expressed in this thesis are mine, not those of the University.



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ONE

Introduction

ONE

Introduction

Resource partitioning and the ecological niche

The ecological niche was first formally described by G. Evelyn Hutchinson (1957). He believed that the niche of a species should define its ecological properties completely, and take into account all physical and biological factors necessary for its survival. Knowing the ecological niche of a species would allow the identification of all the places in the environment where it could exist. The niche is multidimensional, but only applies to a single instant in time, as time is one of the dimensions. Thus, nocturnal and diurnal animals have separate niches, while animals which use some of the same resources have niches which overlap. In theory, sympatric (coexisting) species cannot occupy identical niches, because one would out-compete the other if they did (Hutchinson 1957; Wiens 1989). Niches can be interpreted as parameter combinations in ecological space, and an animal's niche may be reflected in its morphology (Wiens 1989; Wainwright & Reilly 1994).

The distribution of an animal species reflects the pattern of distribution of resources which it needs, the adaptations it has for exploiting those resources (its niche), and the interactions it has with other animals (competition and predation). The presence or absence of a species in a given area may often be explained by these three factors. Therefore, the structure of animal communities, made up of groups of sympatric species, can be described in terms of resource partitioning among its members (Ricklefs 1990). However, many other factors may have influenced the assembly of a community in its evolutionary past, such as chance, the dispersal abilities of animals, habitat changes, speciation and extinction (Wiens 1989).

The role of competition in structuring communities is still disputed by some workers. For example, Letcher *et al.* (1994) conclude that the geographical ranges of

mammals are defined not by competitive exclusion, but by climatic and habitat requirements. Generally though, adaptations leading to resource partitioning are believed to have evolved in response to competition, and communities are considered to be non-random assemblages of species, which are structured by competition throughout their evolution (Fleming 1986; McFarlane 1989; Findley 1993). In a fauna, ecological niches may be densely packed (similar) or more differentiated, depending on the level or intensity of competition experienced in the past. Packing can be seen as a measure of faunal diversity, and densely packed faunas as occupying a smaller area in ecological space than more diverse faunas (Findley 1973). In theory, a high degree of niche overlap is expected to evolve in a community when resources were abundant during its evolutionary past (Wiens 1989).

The structure of bat communities

Bats (Chiroptera) constitute the second most species-rich mammalian order, comprising around 980 species worldwide (Corbet & Hill 1991). Bat species may be chiefly insectivorous, carnivorous, piscivorous, frugivorous, nectarivorous, sanguivorous or omnivorous, and are found in all continents of the world except Antarctica (Hill & Smith 1984). Bats are extremely numerous and species-rich in the tropics (Findley 1993).

The suborder Microchiroptera contains 815 species in 17 families (Corbet & Hill 1991), all of which use echolocation. Unusually for animals of such small size, microchiropteran species are long-lived (up to 30 years), slowly-reproducing animals, which have high adult survivorship (50-80% per year) and maintain relatively stable populations (Hill & Smith 1984). They appear to be adapted to stable communities in which ecological niches are expected to be clearly defined, but greatly overlapping. Numbers of bats in populations are thought to be maintained at levels close to the carrying capacity of the environment, and to be limited more by resources than by competition (Hill & Smith 1984; Findley 1993). In other words, resources available to bats have been abundant in the evolutionary past of bat communities, thus competition was relaxed, and tightly-packed communities have evolved (Wiens 1989). Now, the populations of species in these communities are, theoretically, limited by resources which are shared by many species. One study shows that food availability is probably limiting, at least at some times of the year, for bats in Panama (Bonaccorso 1979).

Field research shows that multiple niche occupancy by bats is indeed a general pattern (Tamsitt 1967; McNab 1971; Fleming 1986). Almost all bat communities have a cluster of densely packed (i.e. similar in niche and morphology) species, as well as fewer outliers (Findley 1976; Findley & Black 1983; Fenton 1990). Because bat communities are densely packed compared to communities of other animals, sympatric bat species are likely to resemble each other closely (Findley 1993).

There are many examples of sibling species among bats, the niches of which are particularly similar. Sibling species are "morphologically similar or identical natural populations that are reproductively isolated" (Mayr 1970). Examples found in Europe include *Myotis myotis* and *Myotis blythii* (Arlettaz & Perrin 1995), *Myotis brandtii* and *Myotis mystacinus* (Taake 1984; Jones 1991), *Plecotus auritus* and *Plecotus austriacus* (Stebbings 1966), and 45 kHz *Pipistrellus pipistrellus* and 55 kHz *Pipistrellus pipistrellus* (two phonic types which are considered to be sibling species in this thesis; Jones & van Parijs 1993; Barratt *et al.* 1995; see 'Thesis overview and conventions used', page 21). In West Africa, *Hipposideros caffer* and *Hipposideros ruber* are sibling species (Jones *et al.* 1993). In North America, *Myotis lucifugus* and *Myotis yumanensis* are very similar and sympatric in some parts of their ranges (Herd & Fenton 1983), and *Myotis keenii* and *Myotis evotis* are sibling species (van Zyll de Jong & Nagorsen 1994).

Some small degree of niche differentiation or competition must have occurred in sympatric species-rich communities and between sibling species (Findley 1993). Detailed ecological studies of sibling species usually document some differences between them (Herd & Fenton 1983; Jones 1991; van Zyll de Jong & Nagorsen 1994), and show that morphologically similar species do not occupy identical ecological niches (Saunders & Barclay 1992), although their niches are usually extremely similar. In a study of bats in Zambia, morphology was found to be strongly predictive of diet (Findley & Black 1983), and this is likely to be generally true. Occasionally, morphologically distinct species may use similar resources if individuals are highly plastic behaviourally (Findley 1973).

Resource partitioning among bats

The elements which define the ecological niches of bats differ from those defining the niches of other mammals and of insectivorous birds. Ecological constraints apply to insectivorous Microchiroptera and place them in a unique position in terms of niche differentiation, because of their three-dimensional hunting habitat, small prey, high

metabolism, nocturnal habit, hibernation and use of echolocation. Bats compete to a limited extent with insectivorous members of the approximately 2.5% (230) of bird species which are mainly nocturnal (Fenton & Fleming 1976). In bats, niche differentiation may be directly apparent, for example as differences in diet, habitat use, microhabitat use, timing of activity, timing of reproduction, differential use of roosts or as differences in predation rate or predation avoidance behaviour. Some of these elements are discussed below. Differences in any of these elements of the niches of species may be apparent in differences in their wing morphology and echolocation call structure, as these dictate which microhabitats the species can exploit, which insects they can detect there, and how far they can fly to reach them (Fenton 1990).

The wing loading of a bat provides a measure of the size of the wings compared to the body (body weight divided by wing area; in N/m^2), and is positively correlated with minimum speed and negatively correlated with manoeuvrability (ability to turn tightly) and agility (ability to turn quickly). The aspect ratio describes the shape of the wings (square of wingspan divided by wing area). High aspect ratio corresponds with long, thin wings and great aerodynamic efficiency in flight. High flight speed at low cost in uncluttered environments requires high wing loading and small pointed wings; manoeuvrability is favoured by low wing loading and short, broad wings (Norberg & Rayner 1987). However, although bats usually fly in the environment predicted from their wing morphology, they may also be flexible and opportunistic in their habitat use. In fact, bats which are adapted to flight in clutter are able to enter open areas, but bats adapted to flight in open areas may not be able to forage in clutter (Brigham, Aldridge & Mackey 1992).

Fast flight in uncluttered environments requires high-intensity, far-ranging echolocation calls, while flight in clutter requires low-intensity, short calls to avoid pulse-echo overlap (Neuweiler 1983; Fenton 1990). Bats which hunt near foliage often use calls of higher frequency than bats which hunt in open spaces. Calls of high frequency attenuate more quickly than those of lower frequency (Lawrence & Simmons 1982), and are therefore unsuitable for the long-range echolocation needed in open spaces (Dusenbery 1992).

Previous studies of resource partitioning among bats have used an ecological approach to document differences in niche (e.g. Fleming, Hooper & Wilson 1972; Black 1974) or a morphological approach, assuming that morphological differences mirror differences in niche (e.g. McNab 1971; Fenton 1972; Freeman 1981b). Studies which use a combination of both (e.g. Aldridge & Rautenbach 1987; Saunders & Barclay 1992) confirm that both approaches are valid, as suggested by Findley & Black (1983), as diet,

echolocation call structure, wing morphology, habitat use and roost choice are all interrelated and have probably co-evolved in bats. They are all aspects of the ecological niches of bat species. Certain combinations of attributes, such as echolocation call structure and wing morphology, are, in theory at least, maladaptive (Aldridge & Rautenbach 1987).

Roosts

Bats use many different types of roost. Night roosts are used for short breaks in foraging and sometimes for perch-hunting. Day roosts can be small shelters used by individual bats, mating roosts (inhabited by males attempting to attract females), or maternity colonies (inhabited by females and their young). Bats roost in caves, in mines, in tunnels, in wells, in holes in eroded banks, in cracks and crevices, under rubble, in buildings, in foliage, in moss, and in modified foliage or tents. Bat species have different requirements for roosts in terms of size, structure and temperature regime. Some species roost clumped together, others singly; some hang from the roof, others flatten themselves against it (Kunz 1982; Hill & Smith 1984). Roost fidelity in bats is linked to the type of roost occupied; high roost fidelity is directly related to roost permanency and inversely related to roost availability (Lewis 1995). Temperate zone bats spend the winter in hibernacula, within which many species have different microclimatic requirements and hibernate in different positions (Bels 1952; Raesly & Gates 1987). Some species migrate seasonally to hibernate (e.g. *Pipistrellus nathusii* and *Nyctalus noctula*; Kapteyn 1995) or to find better foraging sites (e.g. *Lasiurus cinereus;* Findley & Jones 1964 and *Tadarida brasiliensis;* Cockrum 1969). Roost choice may be affected by wing morphology, as bat species with low manoeuvrability may not be able to enter some types of roost. Also, bat populations (Fenton 1970b; Humphrey 1975; Rautenbach, Fenton & Whiting 1996) and the distribution of foraging bats (Tamsit 1967; Kunz 1982) may be constrained by the availability of suitable roosts.

Diet

Different species of insectivorous bat eat different foods (e.g. Ross 1967; Fenton *et al.* 1977; see Chapter 2), and differences may be manifest in the morphology of the teeth and skull. In bats of the family Molossidae, there are Coleoptera specialists with robust skulls and thick jaws, and Lepidoptera specialists with gracile skulls and thin jaws (Freeman 1981a). In 41 species of North American insectivorous bat, jaw morphology corresponds to diet (Freeman 1981b). Different frugivorous bat species also tend to eat different fruits;

in Panama *Artibeus jamaicensis* specialises on the fruits of *Ficus* species, while *Artibeus phaeotis* takes a wider range of fruits (Bonaccorso 1979).

The structure of echolocation calls used by insectivorous bats relates to their diet. For example, bats which feed on Lepidoptera must have specially adapted echolocation calls to avoid being heard, as the tympana of many Lepidoptera are sensitive to the frequencies commonly used by hunting bats (Fenton & Fullard 1981; Rydell, Jones & Waters 1995). *Tadarida teniotis* is adapted, by virtue of its low frequency echolocation calls, to feed on tympanate insects (Rydell & Arlettaz 1994). Bats such as *Plecotus auritus* may also hunt for Lepidoptera and other insects by passive listening (Anderson & Racey 1991).

Wing morphology is reflected in diet. Thus, species of bat which are adapted to gleaning prey from the surfaces of leaves in clutter (such as *Myotis nattereri*; Gregor & Bauerová 1987) are able to feed on diurnal insects resting on leaves during the night, while those adapted to taking prey from the ground (such as *Myotis myotis* and *Myotis blythii*; Arlettaz 1996) can feed on nocturnal ground-dwelling animals. These prey are not available to species which are adapted to hunting by aerial hawking. In fact, insectivorous bats use five distinct foraging strategies, which are defined by Norberg & Rayner (1987). Bats which hunt by fast hawking fly quickly in pursuit of flying insects and rely on speed and agility to catch their prey. Slow hawking bats hunt insects while flying slowly, and detect prey at short range. Trawling bats pick up prey from water surfaces with their hind legs or tail membrane. Gleaning bats take roosting or non-flying prey from leaves or from the ground; many are capable of hovering flight. Perch-hunting or fly-catching bats spend much of the time perched and seeking prey, and fly when they detect prey. Each strategy, if used by a bat, renders different prey species available to it, and the choice of strategy is therefore reflected in the diet. Wing morphology dictates which strategies a species can use, although they are not exclusive, and many species use more than one strategy during normal hunting (Fenton 1990). Wing morphology may also have a more direct influence on the types of insect available to a bat species. *Myotis volans* is able to catch more Lepidoptera than *Myotis lucifugus* even when the two species are hunting in the same habitats, because *Myotis volans* is more manoeuvrable (Saunders & Barclay 1992). In individuals of *Hipposideros ruber* the percentage of Lepidoptera in the diet is positively correlated to the aspect ratio and to the wingspan (Jones *et al.* 1993).

The diet may also vary seasonally, and shift towards the most abundant or energetically rewarding prey items at different times of the year (Heithaus, Fleming &

Opler 1975; Bonaccorso 1979; Jones 1990). Bats may partition food resources by size, rather than by taxonomic division (McNab 1971; Heithaus, Fleming & Opler 1975).

Habitat use

There are differences in large-scale habitat use by species of bat, which result in partitioning of foraging habitat resources (Chapter 4). In Panama, bats which feed on the fruits of *Ficus* species are more often found in closed forest than in open scrubby forest, where mature *Ficus* trees are not abundant (Bonaccorso 1979). In Mexico, the bat species diversity differs between forested and deforested sites, and bats of the subfamily Phyllostominae are more common in forested than in deforested sites (Fenton *et al.* 1992). In Brazil, two adjacent habitats support very different bat faunas. The more topographically diverse habitat supports a more diverse bat fauna (Willig 1983). In Australia, some species (e.g. *Pipistrellus pumilus*) are ubiquitous, whereas others (e.g. *Scotorepens balstoni*) are found only in certain habitats (Fenton 1982). In North America, the bat community of an urban park was found to differ from that of neighbouring rural areas (Kurta & Teramino 1992). In the Netherlands, records of *Myotis mystacinus* are mainly from woodlands, records of *Myotis dasycneme* from canals and rivers, records of *Pipistrellus pipistrellus* from towns and woodlands, while those of *Eptesicus serotinus* are from agricultural areas (Kapteyn 1995). In Scotland, *Myotis daubentonii* and *Plecotus auritus* forage in different habitats even when they occupy the same roost (Swift & Racey 1983).

Bats probably select habitats according to the distribution of suitable prey items (Bonaccorso 1979; Saunders & Barclay 1992; Rautenbach, Fenton & Whiting 1996). The distribution of bats in several habitats in Sweden was attributed to the distribution of swarming insects, and different bat species were found together in insect-rich areas (de Jong & Ahlén 1991). If bat populations are resource-limited as predicted (Hill & Smith 1984; Findley 1993), changes in the area of favoured habitats and the resources found in them would be expected to result in changes in bat populations. There is also some evidence that changes in the configuration of different habitat patches might affect bat populations. Fragmentation of habitats and the isolation of fragments might affect the number of bats or the number of species found in them, and might eventually affect populations of bats (de Jong 1995). Some tropical bat species have relatively small ranges and tend to be sedentary, while others fly long distances between foraging sites (Fleming, Hooper & Wilson 1972). Theoretically, sedentary bat species would be affected more by

habitat fragmentation than more nomadic species, which could fly between suitable habitat patches more easily.

Microhabitat use

Within a habitat, different bat species may hunt in different areas; this is a difference in microhabitat use (see Chapter 5). The wing morphology of a species determines in which areas of a habitat it is able to hunt; gleaning bats can navigate and fly in clutter, while aerial hawkers cannot (Norberg & Rayner 1987; see also page 12 above). In a rain forest in Queensland, Australia, bat species were defined as closed canopy specialists, gap specialists and gap incorporators from activity monitoring and morphological measurements (Crome & Richards 1988). A similar partitioning of microhabitat resources among insectivorous species of bats was observed in southern Africa (Aldridge & Rautenbach 1987). Bat species in south-western Australia were defined as using closed, edge or open habitats based on wing morphology, echolocation parameters and observations (Fullard *et al.* 1991). In forests in Panama, frugivorous species of bat are stratified vertically in terms of microhabitat use; some are most often caught at ground level, some in the canopy (Bonaccorso 1979). Limpens & Kapteyn (1991) theorise that in landscapes consisting of a mosaic of woodland patches and agricultural land, large bat species with intense, far-ranging echolocation calls should be less dependent on the cover and navigational information provided by linear landscape elements such as hedges and wind-breaks than smaller bats with less intense echolocation calls. In a field test of this theory in England, Walsh (1995) showed that *Eptesicus serotinus* is less dependent on linear features than *Pipistrellus pipistrellus*.

Temporal patterns in foraging

There are temporal differences in the foraging activity of some sympatric bat species (Brown 1968; Hill & Smith 1984). For insectivorous and nectarivorous bats, foraging at different times may mean that different resources are available to them, as insects fly at different times of the night and nectar is replenished during the night. For frugivorous bats, temporal differences in foraging may mean that competition at foraging sites is reduced, but only a limited amount of fruit ripens during the day preceding each night and is available on that night (Heithaus, Fleming & Opler 1975). In North America, six species of insectivorous bats have initial foraging periods within five hours after sunset, and two of these five have secondary foraging periods later in the night (Kunz 1973). Two North American bat species which have similar diets seem to change their activity patterns when

they are in sympatry, foraging for a longer period throughout the night than when one species (*Lasionycteris noctivagans*) is found alone (Reith 1980). *Myotis daubentonii* and *Plecotus auritus* emerge and forage at different times in Scotland (Swift & Racey 1983). The time at which bats emerge from day roosts varies greatly between species, and depends on diet and predation risk (as indicated by wing loading) (Jones & Rydell 1994).

The study of foraging habitat use by bats

Because of bats' slow reproductive capacity, long life, high adult survivorship and relative rarity (Harris *et al.* 1995), the activity levels or numbers of bats in foraging habitats are considered to be a good measure of habitat quality (van Horne 1983; Bernstein, Krebs & Kacelnik 1991). Therefore, levels of bat activity in different habitats are measured in order to quantify habitat use and the partitioning of habitat resources among species.

Several methods have been used to survey the bats in a habitat or microhabitat. Early naturalists resorted to the shotgun in order to capture and identify bats, but found them challenging targets. Luckily they could take several shots at each individual, as "bats are fearless creatures and seem wholly unmindful of the fact that the loud explosion disturbing the sunset calm is directed towards them" (Allen 1940). More recently, researchers have used mist nets and harp traps to catch bats alive (Constantine 1958; Tuttle 1974). Mist nets are cheap, lightweight and easily transported and used, but must be tended continuously once erected. Bats are difficult to remove from mist nets without causing them injury. Harp traps are less damaging to bats and do not have to be tended, as captured bats are held in a large bag, but these traps are less portable than nets and have a smaller surface area. They are more suitable for trapping bats leaving roosts, or moving along flyways towards foraging sites, than for capturing those hunting at foraging sites (Kunz 1988). Both nets and traps are usually used under the canopy, and are not very effective for catching high-flying aerial hawking species in their normal foraging sites. Bats which frequent a foraging site may learn to avoid nets put up in the same position on more than one night (Kunz & Brock 1975). Interspecific variability exists in the susceptibility to capture in nets and traps, and in the ability to escape once caught. This results in biases in both methods; large bats are more likely to be caught in nets, while smaller species avoid nets but can sometimes be caught in traps. Echolocation call design may affect bats' susceptibility to nets and traps, and bats may also use vision to detect and

avoid nets. This means that nets and traps used in low light conditions, for instance under the canopy, may have higher capture rates than those placed in open spaces (Francis 1989). Foraging bats may be more easily able to detect nets and traps than bats on flyways between roosts and foraging sites (Thomas & West 1989).

In spite of the biases, catches of bats in nets and traps can be used directly to quantify activity in different habitats. Alternatively, once caught, bats can be equipped with small chemiluminescent tags (Buchler 1976) or transmitters for radio-telemetry (Kunz 1988). These tags can also be used on bats caught at roosts, if the whereabouts of such roosts are known.

Chemiluminescent tags are groomed off quickly by bats, so that observation of foraging behaviour can take place for a few hours at most. During part of this time, the bats' behaviour is likely to be unusual because of recent capture and handling. Also, bats often fly out of sight as soon as they are tagged, and are lost (Barataud 1993). Chemiluminescent tags may be more useful for detailed behavioural observations than for the study of habitat use (Caire *et al.* 1984), although useful information on habitat use by bats tagged with reflective tape has been obtained by large teams of observers (e.g. Racey & Swift 1985).

Collection of habitat data by radio-telemetry is extremely time-consuming, as only one bat can be followed by each researcher on any one night. It is also a relatively expensive method (Hill & Smith 1984). Radio tags used on small (<70g) bats should weigh less than 5% of their body mass (Aldridge & Brigham 1988). Therefore, at present, only the larger bat species found in Great Britain can be safely radio-tagged, because of the weight of the transmitters available. Despite these problems, radio-telemetry has been used successfully to describe movements of bats at foraging sites (e.g. Kronwitter 1988; Jones & Morton 1992; Jones, Duvergé & Ransome 1995).

Since bat detectors have been in use, it has been possible to survey foraging bats acoustically (see Chapter 3). Bat detectors are receivers which transform the ultrasonic echolocation calls used by bats into the audible range. The main advantage of detectors is that bats can be studied without being disturbed. However, it is not possible to recognise or count individual bats from the sounds on a detector; habitat use must always be quantified in terms of bat activity, measured as bat passes. A bat pass is the continuous string of echolocation calls heard on a detector as a bat flies over within range (Fenton 1970a). Species-specific differences in echolocation, shaped by ecology and linked to wing morphology, mean that the identification of bats from echolocation calls is feasible (Norberg & Rayner 1987). However, differences in call intensity and structure and in the

degree of attenuation of different sounds in air mean that the calls of some bat species are easier to hear on a detector than those of others (Lawrence & Simmons 1982; Waters & Jones 1995). Thus, bat detector records are biased towards bats with intense echolocation calls. Bat detector surveys are probably not suitable for the assessment of habitat use by bats with low-intensity echolocation calls, such as the Phyllostomidae (Fenton *et al.* 1992).

Detector surveys of the foraging habitats used by bats can be conducted while transects are walked, cycled, or driven. Bat passes can be recorded for later analysis, or notes can be taken in the field. Alternatively, detectors can be placed at fixed points, and either held in the hand or left to record bats automatically (Thomas & West 1989). There are various types of bat detector and methods for the identification of species of bat from echolocation calls. Bat detectors are not all equally sensitive to bat calls, and the results from different brands of detector cannot be compared directly (Waters & Walsh 1994).

Simple tuneable heterodyne detectors are the cheapest, but bats echolocating outside the narrow frequency band to which the detector is tuned are not heard (Pye 1992). When these narrow-band detectors are used, bats are identified by tuning the detector through the frequencies at which calls can be heard, and listening to subtle differences in the sound. The information on call structure gained from this is combined with visual observations of the flying bats. The method requires skill and experience (Ahlén 1990), and sonagraphic analysis of call structure is not possible, as no frequency information is contained in recordings, and measurement of amplitude and duration parameters from recordings is not reliable (Pettersson 1993). This means that bats must be identified in the field.

There are two broad-band methods for the transformation of bat calls; frequency division and time expansion. Frequency-division detectors are simple and inexpensive but do not retain much detail of call structure. Recordings from frequency-division detectors which retain amplitude can be used to measure duration parameters, but only one harmonic is represented and the frequency resolution of recordings is limited (Pettersson 1993). Time-expansion devices (instrumentation tape recorders and digital capture devices) retain accurate time and frequency information of fundamentals as well as of harmonics (Pye 1992), and the sound reproduction is good (Pettersson 1993). Time-expansion devices are at present the best bat detectors for the analysis of echolocation calls and for the identification of species, because they record all frequencies, and allow detailed sonagraphic analysis of calls (see Chapter 3). Broad-band detectors and the equipment needed for sound analysis are expensive, however.

To conclude, for the study of bat foraging habitat use, the ideal sampling method is one which produces records of bats in proportion to the abundance of each species in the habitat (Francis 1989). A completely unbiased method for sampling bats certainly does not exist. Compared to detector methods, capture methods are more disturbing to bats, and are more prone to site biases which cannot be controlled for in any way (Thomas & West 1989). In general, bat detectors are probably the most appropriate tools for the study of bats in the temperate zone (Kunz & Brock 1975). Acoustic surveys are particularly suitable in Great Britain, where all bat species echolocate and many hunt too high in the sky to be caught easily in mist nets, for which in any case a licence is required.

Bats in Great Britain

All bats are protected by law in the United Kingdom under the Wildlife and Countryside Act 1981 and the Conservation (Natural Habitats 2c) Regulations 1994, as a decline in hibernating and roosting numbers of many bat species has been recorded in the last 40 years in Western Europe (Gaisler, Hanák & Horáček 1980-1981; Weinreich & Oude Voshaar 1992). In Great Britain, there have been few direct studies of bat population changes, but over the last 30 years at least four species have probably undergone significant population declines, and three have declined somewhat (Harris *et al.* 1995). All 16 bat species (including the *Pipistrellus pipistrellus* sibling species) which occur in Great Britain have been found in south-west England, where much of the work described in this thesis was carried out (Jones & Jayne 1988; Arnold 1993; Barlow & Jones 1996).

The family Rhinolophidae is represented by the rare *Rhinolophus ferrumequinum* Schreber, 1774 and by the much smaller and more common *Rhinolophus hipposideros* Bechstein, 1800 (Table 1.1). Both these species have low aspect ratios and high manoeuvrability (Figure 1.1). The family Vespertilionidae is represented by six genera. The sibling species *Myotis brandtii* Eversmann, 1845 and *Myotis mystacinus* Kuhl, 1819 have low aspect ratios, which allow them to fly in woodland clutter. *Myotis nattereri* Schreber, 1818 and the extremely rare *Myotis bechsteinii* Kuhl, 1818 have wing adaptations which allow them to glean prey from surfaces, and *Myotis daubentonii* Kuhl, 1819 is adapted by virtue of low wing loading and large feet to trawling insects from the surfaces of lakes and rivers (Table 1.1; Figure 1.1). *Pipistrellus nathusii* Keyserling & Blasius, 1839, 45 kHz *Pipistrellus pipistrellus*, 55 kHz *Pipistrellus pipistrellus*, and the larger *Nyctalus leisleri* Kuhl, 1818, *Nyctalus noctula* Schreber, 1774 and *Eptesicus*

serotinus Schreber, 1774 have higher aspect ratios and are more efficient in flight (Figure 1.1). These species hunt by aerial hawking. *Pipistrellus nathusii* is more common than previously believed in England (Barlow & Jones 1996). *Plecotus auritus* L., 1758, *Plecotus austriacus* Fischer, 1829 and *Barbastella barbastellus* Schreber, 1774 have low wing loadings and aspect ratios, allowing them to fly slowly in clutter (Figure 1.1). *Plecotus austriacus* and *Barbastella barbastellus* are extremely rare in south-west England (Jones & Jayne 1988; Arnold 1993) and in Great Britain (Table 1.1).

Many of the bat species in Great Britain are largely overlapping in range, size (Table 1.1) and wing morphology (Figure 1.1). All are classed as insectivores, although they sometimes feed on animals other than insects, such as spiders (Norberg & Rayner 1987; see Chapter 2). For all species, the British Isles are on one periphery of their geographical range (Arnold 1993).

The aim of the work presented in this thesis was to describe the way in which the species of bat found in Great Britain partition the foraging habitats available to them (Chapters 4 and 5). To this end, a new method for the identification of bats from broad-band recordings of echolocation calls was devised (Chapter 3). The bats in Great Britain form a densely packed community, the members of which use abundant and similar resources (Chapter 2), but differences in the foraging habitats used by them do exist.

Thesis overview and conventions used

For the purpose of this thesis, the British bat community consists of all 16 microchiropteran species, in two families, which are found in Great Britain (England, Scotland and Wales; Table 1.1). This group of species is referred to as the British bats. Bat taxonomy follows Corbet & Hill (1991) throughout this thesis, except for that of the two phonic types of *Pipistrellus pipistrellus* Schreber, 1774 (Jones & van Parijs 1993; Barratt *et al.* 1995). Although as yet nondescript, the phonic types are here considered to be two sibling species, and are called 45 kHz *Pipistrellus pipistrellus* and 55 kHz *Pipistrellus pipistrellus*. I use *Pipistrellus pipistrellus* to mean both species lumped together or not distinguished from one another. For geographical names I follow the *Times Atlas of the World* (Times Books, London), for spelling the *Oxford English Dictionary* (Clarendon Press, Oxford). Statistical analyses were carried out on Minitab release ten for Windows (Ryan, Joiner & Ryan 1985) with a significance level of 5% (Zar 1984), unless stated to the contrary.

In this thesis I give several direct lines of evidence for foraging resource partitioning among British bat species.

In Chapter 2, I review published and unpublished work on the diets of British bat species. They feed in different ways and eat different foods, but there is a great deal of overlap in the diets and foraging strategies of the commonest species. I conclude that resource partitioning is achieved partly by dietary specialisation, but suggest that the different species may also use different habitats for foraging.

In Chapter 3, I describe a new broad-band acoustic method for the identification of bat species at foraging sites from recordings of their echolocation calls. I discuss the design of echolocation calls in relation to the various foraging strategies and perception techniques used by each species. The method is intended to be used as a tool for the quantification of foraging habitat use by bats in Chapter 4.

In Chapter 4, I describe the results of a broad-scale survey of foraging habitat use by bats. Ten land use types were surveyed for bat activity, using the broad-band identification method described in Chapter 3. Rivers and lakes are the habitats most heavily used for foraging by all bat species, but individual species clearly have habitat preferences, and conservation management schemes should take these into account. Published work on habitat use by bats is reviewed. The management of rivers and lakes for insects is proposed as an effective conservation measure for populations of bats in general.

In Chapter 5, the partitioning of foraging habitat resources by bats is examined on a finer scale in relation to river water quality. Water quality is likely to affect insects emerging from rivers, and therefore also bats. I describe work on the distribution of foraging bats in relation to localised river pollution from treated sewage. I conclude that different species groups of bats would react differently to future changes in river water quality, and use the microhabitat differently.

In Chapter 6, I sum up the data presented in this thesis in relation to resource partitioning by diet and habitat for each of the bat species in Great Britain. The likely effects of future changes in land use on bat species and recommendations for future research and bat conservation policies are also discussed.

Table 1.1 The 16 bat species found in Great Britain, their mid-range forearm length (Fa; Schober & Grimmberger 1987), mean mass (Norberg & Rayner 1987), estimated population and range (number of 1 km^2 squares in which the species has been recorded)(Harris *et al.* 1995). [1] = estimated mean values for males and females, Jones (1991); [2] = mean values, K.E. Barlow, personal communication. Nine species, including the five most common, weigh between 5g and 9g.

Species (abbreviation)	Fa (mm)	Mass (g)	Estimated population	Range (no. squares)
R. ferrumequinum (Rf)	58	23	>4000	114
R. hipposideros (Rh)	40	6.8	14 000	238
M. brandtii (Mb)	35[1]	5.2[1]	30 000	43
M. mystacinus (Mm)	34	5.4	40 000	112
M. bechsteinii (Mbe)	43	10	1500	19
M. nattereri (Mn)	40	7.0	100 000	199
M. daubentonii (Md)	38	7.0	150 000	293
P. nathusii (Pn)	35	6.7	?	?
45 kHz *P. pipistrellus* (45 Pp)	32[2]	5.4[2]	2 000 000	1438
55 kHz *P. pipistrellus* (55 Pp)	32[2]	5.1[2]		
N. leisleri (Nl)	43	17	10 000	41
N. noctula (Nn)	53	27	50 000	199
E. serotinus (Es)	53	22	15 000	128
B. barbastellus (Bb)	40	10	5000	41
P. auritus (Pa)	38	9.0	200 000	436
P. austriacus (Pas)	41	10	1000	19

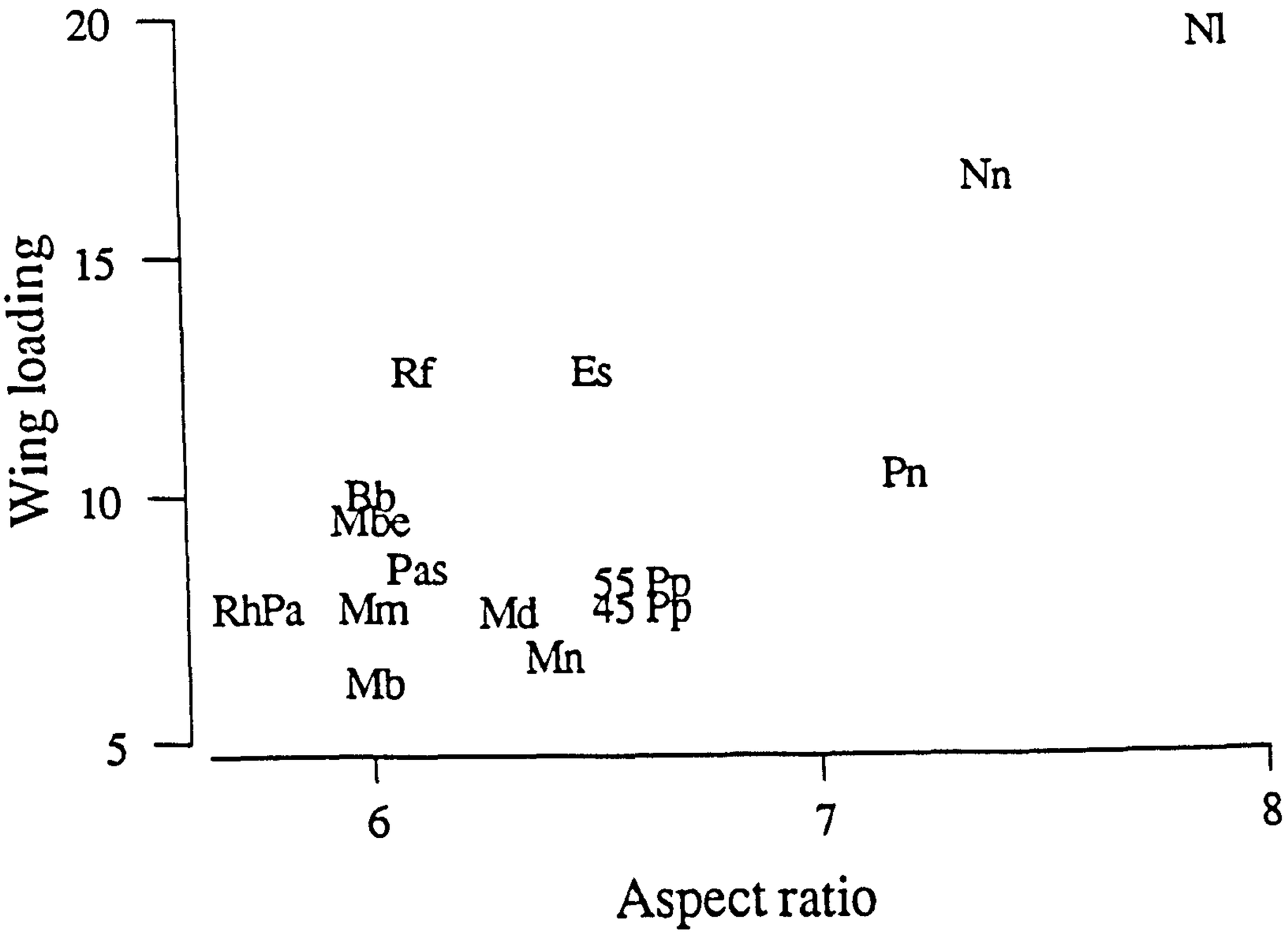


Figure 1.1 A plot of wing loading (weight divided by wing area, in N/m^2) against aspect ratio (square of wingspan divided by wing area) for the 16 British bat species shows that many of them are similar in terms of wing morphology. Abbreviations as in Table 1.1. Sources; Norberg & Rayner (1987); K.E. Barlow (personal communication).

Two

A review of the diets of British bats

Vaughan, N. (1997) The diets of British bats (Chiroptera). *Mammal Review*, in press, is based on this chapter.

Two

A review of the diets of British bats

Summary

I review 61 studies of the diets of 15 bat species found in Great Britain (the diets of 45 kHz and 55 kHz Pipistrellus pipistrellus *are considered together).* Barbastella barbastellus *and* Plecotus *species eat mainly Lepidoptera.* Eptesicus serotinus *takes mainly Coleoptera, but feeds on a wide range of prey, found in several habitats.* Rhinolophus ferrumequinum *takes mainly Coleoptera and Lepidoptera by hawking, gleaning and perch-hunting.* Myotis bechsteinii *feeds mostly on woodland families of Diptera and Lepidoptera. The remaining nine species take mainly Diptera.* Myotis nattereri *takes almost entirely diurnal Diptera, gleaned from their nightly resting places.* Rhinolophus hipposideros *and* Myotis mystacinus *take mostly swarming crepuscular Diptera by hawking, probably near water and in damp wooded areas; both also glean.* Myotis brandtii *feeds on Diptera by hawking and gleaning;* Nyctalus noctula *by hawking.* Myotis daubentonii, Pipistrellus *species and* Nyctalus leisleri *take many aquatic Diptera, and may therefore be expected to feed close to freshwater habitats.* Myotis daubentonii *hunts by trawling aquatic Diptera from the surface of water.*

Introduction

Although various authors have studied the prey of bats, there have been no recent attempts to synthesise all the available data on the food habits of British species (see Mayle 1990 for a brief review). Dietary information can reveal which of the five foraging strategies (Norberg & Rayner 1987; see Chapter 1, page 14) are used by each species of bat, and provide other information about its foraging ecology. For example, bats that can catch and eat tympanate Lepidoptera are likely to use echolocation calls which are not acoustically apparent to them, or hunt by passive listening (Fenton & Fullard 1981; Anderson & Racey 1993; Rydell, Jones & Waters 1995). Bats that eat many insects associated with water or insects with aquatic larval stages (here termed aquatic insects) are likely to be affected by changes in freshwater habitats (see Chapter 5). The presence of non-volant prey (including diurnal prey) in the diet indicates gleaning.

Detailed knowledge of the diets of bats is also important for practical conservation planning and for the interpretation of habitat use surveys (Chapters 4 and 5). Dietary knowledge may also help to explain bat distribution and past changes in bat population sizes, and to predict the effects of future habitat and climate change on bat populations. In this review, I suggest a standard method for future studies. I relate the dietary niche breadth of species of bats to their estimated population sizes in Great Britain.

Conventions used

This review is of the diets of bat species found in Great Britain, though many of the studies were carried out on the continent. Various methods are used to quantify the relative importance of taxa in the diet. Some authors present anecdotal information or details of prey taxa in stomach contents, some give lists of prey remains found under feeding perches, but most present the results of faecal analysis. Several methods are used to quantify the relative dietary importance of prey items in faeces. The percentage occurrence is the percentage of all faecal pellets examined containing each prey taxon (total > 100%; defined by McAney *et al.* 1991). The percentage frequency is the number of occurrences of a taxon (i.e. the number of pellets which contained it), divided by the total number of occurrences, multiplied by 100 (total = 100%; defined by McAney *et al.* 1991). In percentage items, the number of items in the faecal pellets attributed to each prey taxon is

expressed as a percentage of the total number of identified fragments of all taxa, ignoring items which could not be identified (total = 100%). The percentage numbers represents the estimated minimum number of prey animals of each taxon expressed as a percentage of the total estimated minimum number of prey animals per faecal pellet (total = 100%). The percentage animals is the percentage of the total number of animals (of a species of bat), the faeces of which contained a prey taxon (total >100%; as used by Taake 1992). In percentage volume, the prey taxa are given as estimated percentage volume in all faecal pellets (total = 100%).

In Tables 2.1-2.15, the prey taxa eaten are given at the level of Order for adult insects and Class for other prey. For each species of bat, the most commonly eaten insect order or orders are indicated in the table and discussed in more detail (to families) in the text. As far as possible, the extent to which each species feeds on tympanate Lepidoptera, aquatic insects and non-volant prey is described. The identification of lepidopteran families is possible from prey remains found under feeding perches, but difficult from remains in faeces, as often only scales are recovered in droppings (McAney *et al.* 1991). Therefore, many bat species can only be said to eat unspecified Lepidoptera. Prey remains may be biased towards large Lepidoptera, which are carried to feeding perches to be eaten, while smaller moths may be eaten on the wing.

Hard-bodied insects are over-represented and soft-bodied insects are under-represented in faeces (Rabinowitz & Tuttle 1982). Lepidopteran scales remain in the digestive tract for longer than other insect remains and may therefore contaminate later meals (Robinson & Stebbings 1993; Wolz 1993a). Other sources of bias in faecal analysis are described by Kunz & Whitaker (1983) and Dickman & Huang (1988). Although Robinson & Stebbings (1993) conclude that quantitative determination of prey eaten by bats is too inaccurate to be useful, the authors of many studies reviewed here do attempt quantification in various ways, and I summarise their conclusions.

The information given by Poulton (1929) in the last comprehensive review of the diets of British bats is summarised in the tables, but I make no attempt to include data directly from earlier sources. Arthropod taxonomy follows Chinery (1993) and Barnes, Calow & Olive (1993). All information on insect ecology is from Colyer & Hammond (1951), Lewis & Taylor (1964) and Chinery (1993).

The diets of British bats

Rhinolophus ferrumequinum (Table 2.1) eats mainly Lepidoptera and Coleoptera. Lepidopteran families taken include: Noctuidae, Nymphalidae, Hepialidae, Sphingidae, Geometridae and Lasiocampidae (Jones 1990; P.L. Duvergé, personal communication). Noctuidae and Geometridae are tympanate families; members of Nymphalidae are diurnal, and may be taken by bats in roosts. Coleopteran families taken, in order of importance, are: Scarabaeidiae, Geotrupidae, Silphidae (families of dung or carrion beetles likely to be found in pastures) and Carabidae (nocturnal ground beetles). *Rhinolophus ferrumequinum* feeds by hawking, gleaning and perch-hunting (Jones & Rayner 1989).

Rhinolophus hipposideros (Table 2.2) feeds mainly on Diptera. Most dipteran fragments were identified as Nematocera (McAney & Fairley 1989). This sub-order is largely crepuscular and the males of many species form mating swarms on summer evenings. Dipteran families identified were: Tipulidae, Culicidae, Anisopodidae, Chironomidae / Ceratopogonidae (all Nematocera), Stratiomyidae, Empididae, Sphaeroceridae and Muscidae (all diurnal; McAney & Fairley 1989). Four of the nine families are associated with water, two with damp wooded areas. *Rhinolophus hipposideros* feeds by hawking, gleaning (Jones & Rayner 1989) and perhaps by perch-hunting (Ahlén 1988).

Myotis brandtii (Table 2.3) was only distinguished from *Myotis mystacinus* in 1970 (Corbet & Harris 1991), so that early records of the diet of *Myotis mystacinus* must refer to *Myotis brandtii / mystacinus* (Table 2.4). Only Taake (1992; 1993) describes specifically the diet of *Myotis brandtii*, and over 91% of 22 animals he caught had eaten Diptera. 55% had eaten Diptera of the Sub-order Brachycera; these remains were not identified to family level, but most members of the sub-order are diurnal and were probably taken by gleaning. With regard to nematoceran families, 91% of *Myotis brandtii* caught had eaten Tipulidae, 55% Chironomidae, 50% Anisopodidae, 36% Culicidae, 23% unidentified Diptera, 14% Mycetophilidae and 5% Sciaridae. Three of the dipteran families taken are commonly found in damp woodland. 91% of animals had also eaten unidentified Lepidoptera, but as this order is likely to be over-represented in faeces (Robinson & Stebbings 1993), Diptera are considered to be the most important constituent of the diet of *Myotis brandtii.* This species is not particularly reliant on aquatic insects (only Chironomidae and Culicidae have many aquatic members), but does take prey by gleaning (59% of animals had taken Arachnida; Taake 1992; 1993).

Myotis mystacinus (Table 2.4) eats mainly Diptera; of 22 animals caught 96% had eaten Tipulidae, 59% Chironomidae, 41% Anisopodidae, 36% Culicidae, 23% Mycetophilidae, 18% unidentified Diptera, 9% Psychodidae, 5% Cecidomyiidae and 5% Bibionidae (all identified families are crepuscular Nematocera). 82% of animals had eaten unspecified insects of the diurnal Sub-order Brachycera (Taake 1992; 1993). Beck (1994-1995) adds Simuliidae and the diurnal families Muscidae, Syrphidae and Empididae to the list of families taken. In the summer in Germany, *Myotis brandtii* is found near woodland, *Myotis mystacinus* near rivers in more open habitats with hedges and coppices (Taake 1984). Both species take great numbers of Tipulidae, a family found in woodlands. The inclusion of many non-volant prey items in the diet indicates a gleaning habit, and *Myotis mystacinus* takes Diptera from four families associated with water. The similarity in the diets of *Myotis brandtii* and *Myotis mystacinus* is as expected, since these species are very similar in terms of wing morphology and predicted flight behaviour (Jones 1991).

Myotis bechsteinii (Table 2.5) feeds mainly on Lepidoptera (the tympanate family Noctuidae was identified; Wolz 1993b) and Diptera. Of sub-orders of Diptera, Wolz (1993b) found the diurnal Cyclorrhapha in 87% of pellets and the crepuscular Nematocera in 49%. Of families, she found remains of Tipulidae (Nematocera) in 38% of pellets and identified Lauxaniidae and Calliphoridae in one pellet each. Taake (1992; 1993) also found Tipulidae to be the most commonly eaten family (by 77% of 17 bats), while 18% of bats had eaten Anisopodidae and 6% Mycetophilidae. Four of the five dipteran families taken are found in damp areas and woodlands, and none have many aquatic representatives. Non-volant arthropod remains were found in 85% of pellets examined by Wolz (1993b).

Myotis nattereri (Table 2.6) eats mainly diurnal Diptera, which are gleaned from their nightly resting places. Taxa found, in order of importance, were: Muscidae / Anthomyiidae, Brachycera / Calyptratae, Calliphoridae, Syrphidae, Empididae, Dolichopodidae, Fanniidae, Tachinidae, Asilidae / Rhagionidae, Opomyzidae, Sarcophagidae, Tipulidae and Sciaridae (Bauerová & Červený 1986; Gregor & Bauerová 1987). Swift, Racey & Avery (1985) also found mostly Muscidae, and add Anisopodidae to the list. All but two dipteran families identified by Gregor & Bauerová (1987) roost at night, and 68% of the prey by percentage frequency was non-volant according to Shiel, McAney & Fairley (1991). Only a few prey taxa (e.g. Neuroptera and the dipteran Sub-order Nematocera) are perhaps mostly caught by hawking. Several families are often found in woodlands.

Myotis daubentonii (Table 2.7) feeds mainly on aquatic Diptera. Chironomidae (mostly male) appeared in 96% of pellets, while other Diptera (Tipulidae, Culicidae,

Simuliidae, Ceratopogonidae, Mycetophilidae and the diurnal family Empididae) were found in only 2% of pellets (Beck 1994-1995). Male Chironomidae are likely to be found swarming above the water surface, waiting for females to emerge. Similar sex-biased predation, on Lepidoptera by *Lasiurus* species (Acharya 1995) and on Coleoptera by *Rhinolophus ferrumequinum* (Jones 1990), has also been attributed to sexual dimorphism in the flight and mate-seeking behaviour of insects. Sullivan *et al.* (1993) believe that Chironomidae / Ceratopogonidae are the prey most commonly taken by *Myotis daubentonii*, and add the following dipteran families to the list: Anisopodidae, and the diurnal families Rhagionidae, Stratiomyidae, Ephydridae, Sphaeroceridae, Muscidae and Calliphoridae. Swift & Racey (1983) add Cecidomyiidae. *Myotis daubentonii* feeds by trawling insects and pupae (Beck 1994-1995) from the still surfaces of lakes and rivers (e.g. Poulton 1929; Jones & Rayner 1988; Kalko & Schnitzler 1989). Its diet consists mainly of aquatic insects; Chironomidae and seven other families taken are associated with water.

Pipistrellus nathusii (Table 2.8) also appears to take mainly aquatic Diptera. Remains of Chironomidae were found in 100% of pellets examined (Beck 1994-1995), and there is no evidence of gleaning.

Pipistrellus pipistrellus (Table 2.9) takes mainly Diptera; 30% of the diet by frequency was Chironomidae / Ceratopogonidae, 10% was Tipulidae, 7% Psychodidae, 6% Anisopodidae, 6% Empididae, and the remainder was Culicidae and the diurnal families Stratiomyidae, Ephydridae, Sphaeroceridae, Muscidae and Phoridae (Sullivan *et al.* 1993). Hoare (1991), in a study of the diet of *Pipistrellus pipistrellus* during October and November, adds Cecidomyiidae and Trichoceridae to the list of families taken; Beck (1994-1995) adds Simuliidae. Of the 15 families identified in faeces, eight (including Chironomidae and Ceratopogonidae) have fair numbers of aquatic representatives. *Pipistrellus pipistrellus* is reliant on aquatic insects, and often feeds near rivers and lakes (Walsh & Harris 1996). It may take some prey items by gleaning, although the wing morphology of this species suggests that it is better adapted to aerial hawking (Norberg & Rayner 1987).

Nyctalus leisleri (Table 2.10) preys mainly on Diptera; 17% of the diet by frequency was Muscidae, 15% Chironomidae / Ceratopogonidae, 9% Culicidae, 9% Tipulidae, 7% Anisopodidae, and the remainder was Psychodidae, Stratiomyidae and Calliphoridae (Sullivan *et al.* 1993). Waters, Rydell & Jones (1995) found mostly Nematoceran Diptera in droppings. Beck (1994-1995) found Tipulidae to be the most

commonly eaten dipteran family. Of the nine families listed, five include some aquatic insects, but few non-volant prey are taken.

Nyctalus noctula (Table 2.11) eats mainly Diptera, though Coleoptera and Lepidoptera are also important constituents of the diet. Mackenzie & Oxford (1995) identified the following families of Diptera in faeces: the crepuscular Tipulidae, Culicidae and Chironomidae, and the diurnal Muscidae, Syrphidae, Helcomyzidae and Clusiidae. Remains of other families of Diptera identified by Jones (1995) were of Sphaeroceridae, Bibionidae and Sciaridae; coleopteran remains were almost entirely Scarabaeidae. Gloor, Stutz & Ziswiler (1994-1995) found most Chironomidae in faecal pellets to be male, added Trichoceridae and Anisopodidae to the dipteran families eaten, and recorded the coleopteran family Carabidae, members of which are active on the ground at night. Of the 12 dipteran families identified in faeces, only two are aquatic. *Nyctalus noctula* does feed over rivers and lakes, but is not restricted to this foraging habitat (Gloor Stutz & Ziswiler 1994-1995), and is not particularly reliant on aquatic insects. The published identification of lepidopteran families (Noctuidae and Pyralidae) based on wing scale shape has been withdrawn, as morphological characteristics were later found not to be consistent (G.S. Oxford, personal communication). Non-volant prey seem to make up a very small portion of the diet of *Nyctalus noctula*; this supports Howes' (1974a; b) belief that *Nyctalus noctula* occasionally gleans spiders from the ground. However, data on wing morphology suggest that this species is adapted to fast aerial hawking and not to gleaning (Norberg & Rayner 1987).

Eptesicus serotinus (Table 2.12) preys mainly on Coleoptera, but also takes many Lepidoptera and Diptera. Coleopteran families identified, in order of importance, were: Scarabaeidae (Catto, Hutson & Racey 1994), Carabidae, Cerambycidae, Geotrupidae, Elateridae, Curculionidae and Silphidae (Gerber 1994). Lepidopteran families identified by Sologor (1980) were: Zygaenidae (a diurnal family), Tortricidae, Yponomeutidae, Sphingidae, Pyralidae, Geometridae and Noctuidae. Of these, the last three are tympanate. The crepuscular families Tipulidae, Chironomidae (Gerber 1994), Culicidae and Simuliidae (Sologor 1980) appear to be the most commonly eaten families of Diptera, though Mycetophilidae, Sciaridae (Gerber 1994), Bibionidae, Tabanidae, Dolichopodidae, Chloropidae, Muscidae and Calliphoridae (Sologor 1980) are also eaten. The last five families are largely diurnal, and may have been taken by gleaning, perhaps from the ground, as observed by Catto *et al.* (1996). In Germany, *Eptesicus serotinus* is not often found near water, but hunts mainly in the tree canopy (Hildenhagen & Taake 1982). In England, *Eptesicus serotinus* is considered to feed mostly over hay meadows or pasture

(Robinson & Stebbings 1993; Catto, Hutson & Racey 1994), and near white street lamps (Catto *et al.* 1996). In the Ukraine, insects taken by *Eptesicus serotinus* are those of marshy steppe, woodlands, and areas of shrub (Sologor 1980). In fact, this species seems able to use a wide range of habitats for foraging (Gerber 1994). It takes some aquatic insects, and forages by hawking and gleaning.

Barbastella barbastellus (Table 2.13) feeds almost entirely on Lepidoptera, caught during slow hawking. Remains of Arctiidae, a tympanate family, were identified by Sierro & Arlettaz (1995). Remains of spiders and a few plant remains in the faeces suggest that *Barbastella barbastellus* is capable of gleaning (Rydell *et al.* 1996).

Plecotus auritus (Table 2.14) appears, from prey remains, to feed almost entirely on Lepidoptera of the families Noctuidae, Hepialidae, Thyatiridae (Roer 1969), Nymphalidae, Geometridae, Sphingidae, Notodontidae (Krauß 1978), Arctiidae (Thompson 1982) and Pyralidae (Kolb 1958). Of these, six are tympanate and one is diurnal. In the first three studies mentioned above, noctuid remains made up 80-92% of all those identified. Walhovd & Høegh-Guldberg (1984) and Robinson (1990) identified 100 and 99% of prey remains as Noctuidae, and this family of Lepidoptera is tympanate. Of 89 moth remains found by Kurskov (1981), 91% were from tympanate families. Only Bárta (1975) found that the moth family constituting 60% of prey remains was not tympanate (Hepialidae). Faecal analysis reveals the importance of many other taxa in the diet of this species. Of the Diptera, 18% of the diet by frequency was Muscidae, 7% Tipulidae, 5% Anisopodidae, and the remainder was Calliphoridae, Culicidae, Chironomidae / Ceratopogonidae, Psychodidae and Empididae (Shiel, McAney & Fairley 1991). Beck (1994-1995) adds Simuliidae, Sciaridae and Syrphidae to the list of dipteran families eaten. Many items identified in faeces were attributed to non-volant prey (Rydell 1989; Shiel, McAney & Fairley 1991), and six of 12 families of Diptera listed have aquatic members or are found near water as adults.

Plecotus austriacus (Table 2.15) was recognised as distinct from *Plecotus auritus* in 1959 (Corbet & Harris 1991), so that some early studies listed in Table 2.14 must be considered to refer to *Plecotus auritus / austriacus*. Of lepidopteran prey remains, on average 88% were Noctuidae, 3% Geometridae, 2% Arctiidae, 2% Notodontidae and less than 1% were each of Lasiocampidae, Lymantriidae, Drepanidae, Endromidae, Sphingidae and Thyatiridae (Bauerová 1982). Seven of these families are tympanate. In faeces, the following families of Diptera were found: Tipulidae, Anisopodidae, Chironomidae, Mycetophilidae (all crepuscular) and Syrphidae (diurnal; Beck 1994-1995). All except the

aquatic Chironomidae are found in damp woodland. Thus, *Plecotus austriacus* takes almost entirely tympanate Lepidoptera and woodland Diptera.

Discussion

Sources of variation

Intraspecific variation in the diets of bats can be attributed to season (e.g. Labee & Voûte 1983; Bauerová & Červený 1986; Jones 1990; Catto, Hutson & Racey 1994), age (Rolseth, Koehler & Barclay 1994), sex or reproductive status (Belwood & Fenton 1976) and geographic location or presence of other species (Husar 1976). Although evidence is lacking, many of the bat species included in this review may eat different insects on the continent than they do in Great Britain. Not enough information is available at present on these sources of variation in the diets of British bats to allow the discussion of intraspecific variation in this review.

Capture of aquatic insects and tympanate Lepidoptera

In surveys with bat detectors, rivers and lakes are found to support high levels of bat activity (Walsh & Harris 1996; see Chapter 4). Many species of bat are presumed to use these habitats while feeding on emergent insects (see Chapter 5). This review shows that *Myotis daubentonii*, *Pipistrellus* species and *Nyctalus leisleri* are highly reliant on aquatic insects. However, all British species of bat eat some Trichoptera, all of which have aquatic larval stages and adults which remain near water throughout much of their lives, and most species also feed on other aquatic insects.

All 15 bat species also eat Lepidoptera, at least in small numbers. For *Rhinolophus* species, *Myotis brandtii*, *Myotis bechsteinii*, *Nyctalus leisleri*, *Nyctalus noctula*, *Eptesicus serotinus*, *Barbastella barbastellus* and *Plecotus* species, Lepidoptera make up a substantial part of the diet. Tympanate Lepidoptera were identified in the diets of *Rhinolophus ferrumequinum*, *Myotis bechsteinii*, *Barbastella barbastellus* and *Plecotus* species, suggesting that these species use echolocation calls which are not apparent to moths or that they hunt by passive listening (Rydell, Jones & Waters 1995). The echolocation calls of *Rhinolophus ferrumequinum* are of high frequency (82 kHz; see Chapter 3), above the range of most sensitive hearing of Lepidoptera studied to date (Surlykke & Miller 1982; Surlykke 1986). *Plecotus* species probably avoid detection by

moths through hunting by passive listening or through the use of very low-intensity echolocation calls (Anderson & Racey 1993; Rydell, Jones & Waters 1995).

Dietary niche breadth and bat population size

The number of different prey categories taken by each species of bat (counted from Tables 2.1-2.15) is a crude indication of its dietary niche breadth. For example, *Rhinolophus ferrumequinum* takes prey from 11 different categories (Table 2.1). The species with the joint narrowest dietary niche breadth are *Rhinolophus hipposideros* (Table 2.2), *Pipistrellus nathusii* (Table 2.8) and *Nyctalus leisleri* (Table 2.9), each of which take prey from nine categories. The species with the widest dietary niche breadth is *Myotis daubentonii*, which feeds on prey from 16 different categories (Table 2.7). A Spearman rank correlation (Zar 1984) between numbers of prey categories taken by species of bats and their estimated population sizes in Great Britain (as given by Harris *et al.* 1995; see Table 1.1) was significant ($n = 15$, $r = 0.562$, $p < 0.05$). This shows that rare species of bats may have a narrower dietary niche breadth than more common species, as suggested by Greenwood *et al.* (1996), but the relationship is not clear and needs further study. Also, several bat species which are rare in Great Britain are more common where the dietary studies were undertaken, and may take different prey there.

Prey selection

Several authors have compared insect availability in hunting habitats, assessed from catches in traps, with insect remains found in bat faeces (e.g. Labee & Voûte 1983; Swift, Racey & Avery 1985; Jones 1990; Robinson 1990). Comparing insect availability with insects eaten can provide information about prey selection, but even when bats do not take insects in proportion to availability, they may not be actively selecting prey (Arlettaz & Perrin 1995). In field research, some bats do not seem to use echolocation to discriminate between prey-sized items, but attack inedible items as well as insects (Barclay & Brigham 1994). Other authors suggest that bats forage opportunistically on patches of insects, but take prey selectively from within patches (Fenton & Morris 1976), or conform to optimal foraging models by taking the most energetically rewarding food items which they can detect (Fenton & Thomas 1980; Jones 1990).

The issue of prey selection is complicated by biases both in insect trapping (Muirhead-Thompson 1991) and in the assessment of the diets of bats (Robinson & Stebbings 1993; Wolz 1993a). Also, bats probably classify insects by size, hardness (Freeman 1981b), or flight behaviour, rather than by taxonomic division.

The bat community in North America, as investigated by faecal analysis, consists of species that eat mainly Lepidoptera and those that prefer Coleoptera (Ross 1967; Whitaker 1972; Black 1974). Ross (1967) concludes that Diptera are rarely taken, and of 29 bat species mentioned in a review paper, only 11 take more than 10% Diptera (Freeman 1981b). Most African insectivorous bats also feed on Coleoptera and Lepidoptera (Aldridge & Rautenbach 1987). In Great Britain the damp climate, with relatively little difference between summer and winter temperatures, may be favourable for the survival of Diptera. Indeed, of all insects caught in two light traps set up every night in England for four years, 87% were Diptera, 10% were Lepidoptera, and the remaining 3% were other orders (Williams 1939). This may explain why, for ten of the 15 British species of bats, Diptera appears to be the most commonly eaten order.

Conclusions

Myotis bechsteinii feeds mainly by gleaning, and takes families of Diptera found in woodland as well as Lepidoptera. *Myotis nattereri* takes almost entirely diurnal Diptera, gleaned from their nightly resting places in woodland or near water. Both these species also glean many spiders. *Rhinolophus hipposideros*, *Myotis brandtii* and *Myotis mystacinus* take mostly swarming crepuscular Diptera by hawking, although they also glean diurnal Diptera. Dipteran families taken by these species are found near water and in damp wooded areas. *Nyctalus noctula* hunts Diptera by hawking. *Myotis daubentonii*, *Pipistrellus* species and *Nyctalus leisleri* eat many aquatic Diptera, and may therefore be expected to forage near rivers and lakes. *Myotis daubentonii* hunts by trawling aquatic Diptera from the surface of water. *Barbastella barbastellus* and *Plecotus* species eat mainly tympanate Lepidoptera. *Eptesicus serotinus* takes mainly Coleoptera, but feeds on a wide range of prey found in several habitats. *Rhinolophus ferrumequinum* takes mainly Coleoptera and Lepidoptera by hawking, gleaning and perch-hunting.

Many bat faunas include examples of sympatric species, the ecological niches of which appear to overlap in many dimensions (e.g. Herd & Fenton 1983; Saunders & Barclay 1992; Arlettaz & Perrin 1995; see Chapter 1). This review shows that in the British bats, some niche differentiation occurs through diet and foraging strategy, but there is considerable overlap. Not enough is known about the foraging ecology of British bats to be able to understand fully how they avoid competition for prey, while so many species rely heavily on Diptera for food. Rare bats may exploit a narrower range of prey categories than common species, but this hypothesis needs to be tested when more data have been collected.

Recommendations

Many different and incompatible methods of assessing the relative importance of prey taxa in the diets of bats are used in the studies reviewed in this chapter. In future studies, authors should follow the methods described by McAney *et al.* (1991) for insect identification, but give prey taxa both as percentages of the faecal volume and as percentage items (the number of items of each prey taxon as a percentage of the total number of identified remains). The use of these methods, in which the total diet equals 100%, allows percentages for families to be aggregated into percentages for orders, if desired for comparison with other studies. This is not possible when the prevalence of a taxon in the diet is expressed as the percentage occurrence. The introduction of unnecessary biases into the assessment of diets, for example by the estimation of minimum numbers of insects contained in each faecal pellet (here called percentage numbers), should be avoided. When faecal samples can be attributed to individual bats (e.g. when bats are caught in mist nets and held in bags for the collection of pellets), care should be taken to avoid pseudoreplication (Hurlbert 1984). In other words, the sample size should be the number of bats, not the number of faecal pellets.

I recommend that the diets of rare and poorly studied bat species should be investigated. A comparative study of the diets of 45 kHz and 55 kHz *Pipistrellus pipistrellus* is already under way (K.E. Barlow, personal communication). Intraspecific variation in diets should be considered, and studies of species in allopatry and in sympatry should be carried out in order to evaluate the effects of competition.

Key to abbreviations in the tables.

Methods (see 'Introduction' for details):

an = anecdotal evidence or direct observation of feeding bats,

fa = faecal analysis,

pr = prey remains found under feeding perch or in roost,

sc = stomach contents,

% a = percentage animals (total >100%),

% f = percentage frequency (total = 100%),

% i = percentage items (total = 100%),

% n = percentage numbers (total = 100%),

% o = percentage occurrence (total > 100%),

% v = percentage volume (total = 100%),

n = number of animals, pellets or prey remains.

Prey taxa (those in bold text in the tables are considered to be the most important):

C.Ga. = Class Gastropoda

C.Ar. = Class Arachnida

C.Ch. = Class Chilopoda

C.I.L. = Class Insecta larvae

C.Br. = Class Branchiopoda

C.Os. = Class Ostracoda

C.Oy. = Class Osteichthyes.

Eph. = Ephemeroptera

Odo. = Odonata

Plec. = Plecoptera

Orth. = Orthoptera

Der. = Dermaptera

Dic. = Dictyoptera

Pso. = Psocoptera

Hem. = Hemiptera

Thy. = Thysanoptera

Neu. = Neuroptera

Col. = Coleoptera

Dip. = Diptera

Lep. = Lepidoptera

Tri. = Trichoptera

Hym. = Hymenoptera

✓ = present in diet, ✓✓ = important in diet.

Table 2.1 The diet of *Rhinolophus ferrumequinum*.

Source	Location	Methods	*n*	C.Ar.	Der.	Pso.	Hem.	Thy.	Neu.	**Col.**	Dip.	**Lep.**	Tri.	Hym.
Poulton 1929	England	fa, % o	41	7%						66%	25%	68%	3%	3%
Hooper 1962	England	pr	?	✓						✓		✓		
Leishman 1983	England	fa, % o	80				3%		15%	88%	66%	86%*	15%	25%
Zahner 1984	Germany	fa	1300						✓	✓	✓	✓		✓
Robertson 1988	England	fa, % o	540						1%	50%	✓✓	75%		✓
		pr	97							73%	6%	21%		
Jones 1990	England	fa, % v	540		✓					33%	18%	41%		8%
		pr	>200							✓	✓	✓		
ASHG 1994	Switzerland	fa, % o	260	<5%		<5%	<5%		<5%	52%	44%	47%	<5%	40%
Pir 1994	Luxembourg	fa, % o	160	1%				1%	6%	34%	61%	79%	35%	28%
Beck 1994-1995	Switzerland	fa, % o	164	1%			1%		5%	24%	25%	78%	12%	29%
Boonman 1996	Belgium	fa, % n	92	2%					3%	53%	24%	16%	2%	
Ransome 1996	England	fa, % v	2000							42 %	13 %	40 %		4 %
Duvergé pers. comm.	England	fa, % v	1480						<1%	36%	16%	40%	<5%	7%
		pr	449		<1%				1%	81%	5%	10%	1%	1%

* adults and larvae.

Table 2.2 The diet of *Rhinolophus hipposideros*.

Source	Location	Methods	*n*	C.Ar.	Pso.	Hem.	Neu.	Col.	**Dip.**	Lep.	Tri.	Hym.
Poulton 1929	England	pr	?	✓					✓	✓✓		
Leishman 1983	England	fa, % o	55			2%	36%	9%	80%	89%	31%	35%
McAney & Fairley 1989	Ireland	fa, % f	630	3%		1%	13%	3%	41%	19%	18%	4%
Hollyfield 1993	England	fa, % n	240			2%	14%		44%	35%	1%	3%
Beck *et al.* 1989; Beck 1994-1995	Switzerland	fa, % o	880		3%	1%	37%	2%	76%	63%		3%
		pr	11				✓	✓	✓			

Table 2.3 The diet of *Myotis brandtii*.

Source	Location	Methods	*n*	C.Ar.	C.I.L.	Eph.	Pso.	Hem.	Neu.	Col.	**Dip.**	Lep.	Tri.	Hym.
Taake 1992; 1993	Germany	fa, % a	22	59%	5%	5%	14%	>14%	50%	18%	>91%	91%	36%	>32%

Table 2.4 The diet of *Myotis mystacinus*.

Source	Location	Methods	*n*	C.Ar.	C.I.L.	Eph.	Plec.	Pso.	Hem.	Neu.	Col.	**Dip.**	Lep.	Tri.	Hym.
Poulton 1929*	England	an	-			✓					✓	✓	✓		
Nyholm 1965*	Finland	pr	?			✓	✓				✓	✓	✓✓	✓	
Kurskov 1968*; 1981	Belarus	fa, pr, sc	?			✓	✓				✓	✓✓	✓	✓	
Taake 1992; 1993	Germany	fa, % a	22	82%	5%	5%	5%	9%	>32%	>32%	23%	>96%	77%	59%	9%
Hollyfield 1993	England	fa, % n	119	6%						3%	4%	49%	35%		2%
Beck 1994-1995	Switzerland	fa, % o	80	26%					3%	8%	3%	86%	14%		4%

* *Myotis brandtii / mystacinus.*

Table 2.5 The diet of *Myotis bechsteinii*.

Source	Location	Methods	*n*	C.Ar.	C.Ch.	C.I.L.	Orth.	Der.	Dict.	Hem.	Neu.	Col.	**Dip.**	**Lep.**	Tri.	Hym.
Kolb 1958	Germany	fa	?									✓	✓			
Taake 1992; 1993	Germany	fa, % a	17	>47%	18%	24%	12%			>35%		59%	>77%	>53%	12%	12%
Wolz 1993b	Germany	fa, % o	177	>37%	26%		25%	21%	28%	>27%	46%	36%	87%	97%*		19%

* adults and larvae.

Table 2.6 The diet of *Myotis nattereri*.

Source	Location	Methods	*n*	C.Ar.	C.Ch.	C.I.L.	Eph.	Plec.	Orth.	Der.	Pso.	Hem.	Neu.	Col.	**Dip.**	Lep.	Tri.	Hym.
Poulton 1929	England	an	-												✓	✓		
Kurskov 1968; 1981	Belarus	fa, pr, sc	?					✓						✓	✓✓	✓	✓	
Bauerová & Červený 1986	Czech Rep.	fa, % v	±700	7%				<1%	<1%	<1%		1%	2%	41%	42%	4%*	1%	2%
Shiel *et al.* 1991	Ireland	fa, % f	200	18%	1%					1%		3%		5%	43%	5%	13%	11%
Taake 1992; '93	Germany	fa, % a	14	>71%		14%				7%	7%	14%	29%	71%	>86%	36%	7%	>14%
Whitaker *et al.* 1994	Israel	fa, % v	2	10%								43%		43%	5%			
Beck '91;'94-'95	Switzerland	fa, % o	410	38%		2%	3%			1%		7%	3%	5%	81%	30%	1%	4%

* adults and larvae.

Table 2.7 The diet of *Myotis daubentonii*.

Source	Location	Methods	*n*	C.Ar.	C.I.L.	Eph.	Plec.	Orth.	Pso.	Hem.	Neu.	Col.	**Dip.**	Lep.	Tri.	Hym.	C.Br.	C.Os.	C.Oy.
Poulton 1929	England	an	-												✓				
Nyholm 1965	Finland	pr	?										✓✓	✓	✓				
Brossett & Debouttéville 1966	France	fa	?	✓						✓			✓✓	✓	✓	✓	✓	✓	✓
Kurskov 1968; 1981	Belarus	fa, pr, sc	?			✓	✓						✓✓	✓	✓				
Swift & Racey 1983	Scotland	fa, % i	75			2%					<1%	2%	57%	2%	36%				
Taake 1992; '93	Germany	fa, % a	36	33%	3%	3%		6%	3%	3%	17%	33%	>92%	33%	8%	8%			
Sullivan *et al.* 1993	England	fa, % f	161	8%		3%			<1%	9%		1%	42%	4%	30%	1%			
Beck 1994-'95	Switzerland	fa, % o	306			1%	2%		1%	21%	14%	5%	99%*	3%	7%	3%	✓		

* including Chironomidae pupae.

Table 2.8 The diet of *Pipistrellus nathusii*.

Source	Location	Methods	*n*	Eph.	Plec.	Hem.	Neu.	Col.	**Dip.**	Lep.	Tri.	Hym.
Kurskov 1968; 1981	Belarus	fa, pr, sc	?	✓	✓		✓	✓	✓✓	✓	✓	
Taake 1992; 1993	Germany	fa	2						✓✓			
Beck 1994-1995	Switzerland	fa, % o	105			5%	2%		100%	1%	5%	1%

Table 2.9 The diet of *Pipistrellus pipistrellus*.

Source	Location	Methods	*n*	C.Ar.	Eph.	Plec.	Pso.	Hem.	Neu.	Col.	**Dip.**	Lep.	Tri.	Hym.
Poulton 1929	England	an	-								✓	✓		
Kurskov 1968; 1981	Belarus	fa, pr, sc	?		✓	✓			✓	✓		✓✓	✓	
Swift *et al.* 1985	Scotland	fa, % n	?*		3%				1%	<1%	69%	1%	26%	
Hoare 1991	England	fa, % n	>70								99%	2%		
Sullivan *et al.* 1993	Ireland	fa, % f	160	2%	1%		<1%	1%	2%	1%	66%	5%	16%	7%
Beck 1994-1995	Switzerland	fa, % o	60					33%	18%		65%	33%		22%

* faeces from 112 bats were analysed.

Table 2.10 The diet of *Nyctalus leisleri*.

Source	Location	Methods	*n*	C.Ar.	Eph.	Hem.	Neu.	Col.	**Dip.**	Lep.	Tri.	Hym.
Poulton 1929	England	an, sc	?					✓	✓✓	✓	✓	
Sullivan *et al.* 1993	Ireland	fa, % f	220	<1%	1%	<1%	1%	7%	58%	11%	21%	1%
Waters 1994	England	fa, % v	50	✓				42%	48%	10%		
Beck 1994-1995	Switzerland	fa, % o	126				5%	1%	39%	67%	15%	3%
Waters *et al.* 1995	England	fa, % v	100					8%	77%	12%	✓	

Table 2.11 The diet of *Nyctalus noctula*.

Source	Location	Methods	*n*	C.Ar.	Eph.	Plec.	Orth.	Hem.	Thy.	Neu.	Col.	Dip.	Lep.	Tri.	Hym.
Poulton 1929	England	an	-		✓						✓✓				✓
Kolb 1958	Germany	fa	?				✓				✓		✓		
Kurskov 1968; 1981	Belarus	fa, pr, sc	?								✓✓	✓✓	✓✓		
Howes 1974a; b	England	fa	±200	✓							✓	✓			✓
Beck 1994-1995	Switzerland	fa, % o	130	2%	19%	3%		38%		4%	19%	44%	19%	34%	13%
Gloor *et al.* 1994-1995	Switzerland	fa, % o	435	1%	9%			9%		18%	18%	46%	28%	48%	3%
Jones 1995	England	fa, % v	240								44%	22%	18%		
Mackenzie & Oxford 1995	England	fa, % v	110	<1%				1%	<1%	1%	18%	44%	36%		<1%

Table 2.12 The diet of *Eptesicus serotinus*.

Source	Location	Methods	*n*	C.Ga.	C.Ar.	Odo.	Eph.	Orth.	Dic.	Hem.	Neu.	Col.	Dip.	Lep.	Tri.	Hym.
Poulton 1929	England	an	-									✓		✓		
Kurskov 1968; 1981	Belarus	fa, pr, sc	?					✓				✓✓	✓	✓✓		
Sologor 1980	Ukraine	fa, % i	?									>22%	>62%			
		sc, % i	29									<96%	<38%			
		fa & sc	?	✓	✓	✓	✓	✓	✓	✓	✓	✓✓	✓✓	✓	✓	✓
Kurtze 1982	Germany	fa, % i	?									33%	6%	50%	✓	✓
Labee & Voûte 1983	Netherlands	fa	±130							✓	✓	✓✓	✓✓	✓✓	✓	
Robinson & Stebbings 1993	England	fa, % o	408							12%	3%	96%	10%	15%	<1%	14%
Gerber 1994	Switzerland	fa, % o	1640		<1%			<1%		22%	9%	70%	21%	47%	31%	21%
Catto *et al.* 1994	England	fa, % i	750									66%	19%	4%		6%
Beck 1994-1995	Switzerland	fa, % o	115		2%					17%	3%	53%	32%	34%	25%	13%

Table 2.13 The diet of *Barbastella barbastellus*.

Source	Location	Methods	*n*	C.Ar.	Eph.	Pso.	Hem.	Neu.	Col.	Dip.	**Lep.**	Tri.	Hym.
Kurskov 1968; 1981	Belarus	fa, pr, sc	?		✓			✓	✓	✓✓	✓✓	✓	
Beck 1994-1995	Switzerland	fa, % o	80			1%		6%		9%	99%		3%
Sierro & Arlettaz 1995	Switzerland & Asia	fa, % v	246					<1%		<1%	99%	<1%	
Rydell *et al.* 1996*	Germany	fa, % v	40					✓		9%	88%	✓	
	Switzerland	fa, % v	80				✓			4%	94%		
	Switzerland	fa, % v	80	3%			✓		✓	18%	73%		✓

* droppings were collected at 3 maternity roosts.

Table 2.14 The diet of *Plecotus auritus*.

Source	Location	Methods	*n*	C.Ar.	C.Ch.	Eph.	Plec.	Orth.	Der.	Pso.	Hem.	Neu.	Col.	Dip.	**Lep.**	Tri.	Hym.
Poulton 1929*	England	an, pr	>799										✓	✓	✓✓		
Buckhurst 1930*	England	pr	80												100%		
Manwaring Baines 1939*	England	pr	?												100%		
Hanson 1950	Sweden	pr	1020					<1%					2%	<1%	98%	1%	<1%
Kolb 1958*	Germany	fa	?										✓		✓		
Kurskov 1968; 1981	Belarus	fa, pr, sc	?			✓✓	✓✓					✓✓	✓	✓✓	✓✓	✓✓	
Roer 1969	Germany	pr	37												100%		
Bárta 1975	Slovak Rep.	pr	97												100%		
Heinicke & Krauß 1978	Germany	pr	266												100%		
Krauß 1978	Germany	pr	623					<1%						<1%	100%		
Thompson 1982	England	pr	969												100%		
Swift & Racey 1983	Scotland	fa, % i	125	5%					1%		1%	1%	22%	13%	41%	16%	
Walhovd & Høegh-Guldberg 1984	Denmark	pr	162												100%		
Rydell 1989	Sweden	fa, % v	300	18%					7%				8%	29%	27%	9%	
Oldfield 1990	England	fa, % f	180	21%†					? †		6%	1%	<1%	14%	21%	22%	
		pr	93												100%		
Robinson 1990	England	pr	730						<1%			<1%	3%	2%	93%	2%	
Shiel *et al.* 1991	Ireland	fa, % f	200	12%	6%				4%		1%	1%	5%	33%	27%	11%	2%
Taake 1992; 1993	Germany	fa, % a	31	>16%					26%		3%	>16%	45%	>39%	74%	10%	
Hollyfield 1993	England	fa, % n	240	3%								1%	6%	20%	68%		
Beck 1994-1995	Switzerland	fa, % o	854	2%	1%		1%	1%	17%	5%	5%	4%	8%	57%	61%		4%
Boonman 1995	Netherlands	fa, % n	68								6%	3%	25%	29%	30%		4%

* *Plecotus auritus / austriacus.*

† Many remains classified by Oldfield (1990) as Dermaptera actually belonged to Class Arachnida, so that the true percentage of Dermaptera is unknown. At least 21% of the diet by frequency consisted of correctly identified remains of Class Arachnida (D.W. Yalden, pers. comm.).

Table 2.15 The diet of *Plecotus austriacus*.

Source	Location	Methods	*n*	C.Ar.	C.Ch.	Der.	Pso.	Hem.	Neu.	Col.	Dip.	**Lep.**	Tri.	Hym.
Bauerová 1982	Czech Republic	fa	35 g					✓	✓	✓	✓	✓✓	✓	✓
		pr	4000							✓		88%		
Whitaker *et al.* 1994	Israel	fa, % v	5									100%		
Beck 1994-1995	Switzerland	fa, % o	1113	<1%	<1%	1%	<1%		4%	17%	43%	90%		4%

THREE

Identification of British bat species by multivariate analysis of echolocation call parameters

A paper based on this chapter has been submitted to *Bioacoustics.*

THREE

Identification of British bat species by multivariate analysis of echolocation call parameters

Summary

*A method for the identification of bat species from time-expanded broad-band recordings of their echolocation calls is presented. The method is used for the assessment of habitat use by bats in the work described in Chapter 4. Recordings were made of echolocation calls produced by 536 bats of known species identity, belonging to 15 British species. One call was analysed per individual, and sonagrams and descriptive statistics of six time and frequency parameters of calls are presented. British bats could be placed in three groups according to the structure of their calls. Bats in the first group (*Rhinolophus *species) could be identified unambiguously from the peak frequency of their high duty cycle, predominantly constant-frequency calls. Multivariate discriminant analyses were carried out on time and frequency parameters of calls of the remaining two groups of bats. Of calls of bats in the second group (*Myotis *species and* Plecotus *species), 67% could be correctly identified. These bats produced calls which were frequency modulated and of low duty cycle. The bats in the third group (*Pipistrellus *and* Nyctalus *species and* Eptesicus serotinus*) could be correctly identified from their calls in 89% of cases. These calls had a frequency-modulated component and a constant-frequency component, and were of intermediate duty cycle.*

Introduction

The assessment of the foraging habitats used by bats requires the identification of bats in flight at their foraging sites. Several authors have described methods for the identification of bats in flight from combined visual and acoustic observations (e.g. Hooper 1969; Ahlén 1981; Weid 1988; Ahlén 1990). However, methods that involve visual identification rely on the experience of the observer and on the ability to observe the individual bat which is heard on the detector. Narrow-band heterodyne detectors are often used, bats calling outside the tuned frequency range are missed, and sonagraphic analysis of calls is not possible (Pye 1992). The methods are subjective, and their success rate in bat identification cannot be quantified. In habitats where many bats are present, identification of bats is extremely difficult using these methods (Hooper 1969; see Chapter 1 page 19).

Broad-band acoustic methods (frequency division and time expansion; Chapter 1 page 19) have been used to describe calls for species identification purposes, for example by Fenton & Bell (1981) and Weid & von Helversen (1987). Zingg (1990) attempted to quantify the interspecific variability of frequency-divided echolocation calls by multivariate analysis, so that the degree of accuracy of species identification could be assessed.

Interspecific variation in echolocation calls reflects differences in wing morphology, flight and hunting behaviour, which are shaped by ecology (Neuweiler 1989). Across species, the frequency of echolocation calls scales with body mass (Barclay & Brigham 1991; Jones 1996a), as does the pulse repetition rate (Jones 1994). Thus, I expect to find interspecific differences in echolocation call design. These differences mean that the identification of bats from echolocation calls is feasible.

My aim in this chapter was to describe a method for the classification of echolocation calls, recorded in the field after time expansion, to bat species. Multivariate discriminant analysis was carried out on a database of calls of known species origin, to develop a model which can be used for the classification of new calls recorded for the habitat survey described in Chapter 4. This is the first application of multivariate methods to parameters of time-expanded bat echolocation calls, and the first attempt to quantify the classification of calls made by *Myotis* species. Calls made by bats of this genus are very similar in structure.

Methods

Recording equipment

Two bat detectors (Ultra Sound Advice, London; S-25) were linked to a Portable Ultra Sound Processor (Ultra Sound Advice, London; PUSP) and a Professional Walkman (Sony, Tokyo; WM-D6C). Detector 1 was set to frequency division, and its output was recorded on Channel 1 of the Walkman. The high frequency output from Detector 2 was time expanded (10x) by the PUSP and the output was recorded on Channel 2 of the Walkman. The sampling rate of the PUSP was 448 kHz. The bat detector microphone had a frequency response of -57 dB ± 3 dB (ref. 1 V/μbar) from 20-120 kHz, the Walkman ± 3 dB from 40 Hz-15 kHz. Recordings were made on 90-minute metal tapes (Sony, Tokyo; metal XR). Only the time-expanded recordings made on Channel 2 were used for the analysis described in this chapter. The frequency-division recordings made on Channel 1 were used for the work described in Chapter 5.

Recording calls of known species identity

I recorded echolocation calls outside maternity roosts where bats had been previously caught and identified in the hand, and when bats were released from the hand, in the summers of 1993-1995 in England and Wales. I recorded calls produced by 15 species of British bat; only *Plecotus austriacus* calls were not recorded. Some recordings of two species were made during free flight in the field, but only at a well-known foraging site where bats could be watched foraging in a distinctive way (Jones & Rayner 1988) and had been previously caught and identified in the hand (two individuals of *Myotis daubentonii*), or when the bats could be identified with the aid of species-specific social calls (all individuals of *Pipistrellus nathusii*; Barlow & Jones 1996). For all recordings, the PUSP was activated once as an individual bat flew over, as it is impossible to time-expand continuously. Thus 20 seconds of search phase (Griffin, Webster & Michael 1960) echolocation calls were recorded for each bat, representing two seconds in real time. This was considered to be a random sample of echolocation calls from a bat pass (Fenton 1970a; see Chapter 1 page 18).

To collect recordings of bats leaving roosts at dusk, I visited each roost on one evening only. This was to ensure, as far as possible, that each bat was recorded only once. Where possible, I recorded many calls of each species at several geographical locations,

and made recordings near vegetation as well as further away from clutter. This was done so that the intraspecific variation in echolocation calls due to geographical location (Thomas, Bell & Fenton 1987) and hunting habitat (Miller & Degn 1981; Zbinden 1989; Kalko & Schnitzler 1993; Obrist 1995) would be represented in the data.

Sound analysis and statistical analysis of six call parameters

The tapes were analysed using a Digital Sound Processing Sonagraph (Kay Elemetrics, Pine Brook, New Jersey, USA; 5500, 512 pt. fast fourier transform with Hamming window, 400 Hz frequency resolution). From each downloaded sequence of echolocation calls made by an individual bat, usually the second call was analysed. Only one call per bat was used, in order to avoid pseudoreplication (Hurlbert 1984). In some cases the second call could not be used because echolocation calls made by other bats obscured it, so I used the penultimate call of the bat pass sample. Rarely, only one call was suitable for analysis, so this call was used. Six parameters were measured from the harmonic containing most energy of the call. This harmonic was used, because I anticipated that in some field recordings, the harmonic containing most energy would be the only one of high enough intensity to measure parameters from. The duration of the call (ms) and the interpulse interval (the time between the start of the call and the start of the next call; ms) were measured from waveforms. The peak frequency (frequency of maximum energy), start frequency, end frequency and centre frequency (peak frequency at half the call's duration) were measured from sonagrams in kHz.

Variation in echolocation call structure was investigated using multivariate analysis and correlation. Parameters from calls of individual species were rarely found to conform to the multivariate normal distribution (Box's M test; Mardia, Kent & Bibby 1994), but discriminant functions are quite robust to departures from normality, which are likely to reduce performance slightly (Dillon & Goldstein 1984). Multivariate Analysis of Variance (MANOVA) was used to establish values for Wilks' λ and to calculate communalities for echolocation call parameters. Covariance matrices were found to be heterogeneous, so the quadratic discriminant function was used (Dillon & Goldstein 1984). Parameters from the calls of known identity were submitted to this analysis so that echolocation calls subsequently recorded in the field could be allocated to a bat species with a known degree of certainty. Results of analyses carried out on Minitab release ten for Windows (Ryan, Joiner & Ryan 1985) and on software designed and written by Prof. J.M.V. Rayner were identical.

Results

The echolocation calls of each of the 15 species recorded are described in terms of the six parameters measured (Table 3.1).

The calls fell into three groups in terms of structure. Calls produced by *Rhinolophus* species at high duty cycles (56-60%) were predominantly of constant frequency, but had frequency-modulated sweeps at the start and end (FM/CF/FM calls; Figure 3.1). Most of the energy was invariably contained in the second harmonic. Calls produced by *Myotis* species and *Plecotus auritus* at low duty cycles (2-4%) were frequency modulated (FM calls; Figure 3.2). Most of the energy was contained in the fundamental, except in calls of *Plecotus auritus*, which sometimes had more energy in the second harmonic. The calls of *Pipistrellus* and *Nyctalus* species and *Eptesicus serotinus* had a frequency-modulated component, then a constant-frequency component and were of intermediate duty cycle (4-6% ; FM/CF calls; Figures 3.3 and 3.4). Most of the energy was contained in the fundamental. Within the last two groups, there was overlap in time and frequency parameters, so that unknown calls could not be assigned to a species without multivariate discriminant analysis.

A call of one individual of *Barbastella barbastellus* is included in Table 3.1, but I do not attempt to allocate the calls of this species to a group. Some of the calls I recorded from this individual were similar to FM calls described above, but others swept up and then down in frequency (Figure 3.2). I am unsure which calls are used in normal search phase flight.

The relationship between peak frequency and mid-range forearm length (Schober & Grimmberger 1987) is shown in Figure 3.5. For bats with low and intermediate duty cycles (< 6%) and most energy in the fundamental (all bats except *Rhinolophus* species), there is a significant correlation (n = 13; Pearson's correlation coefficient = -0.734; $P < 0.01$; Zar 1984). Large bats produce calls of lower frequency than small bats.

FM/CF/FM calls

There was no overlap between the peak frequencies of calls made by *Rhinolophus ferrumequinum* (mean peak frequency 82 kHz) and *Rhinolophus hipposideros* (mean peak frequency 109 kHz), so that calls of these species could be classified unambiguously (see Figure 3.1).

FM calls

When the six parameters were submitted to quadratic discriminant analysis with specified prior probabilities and cross validation, 67% of 233 calls made by *Myotis* species and *Plecotus auritus* were reclassified correctly to one of the five species (Table 3.2). Random classification would have been approximately 20% correct. A MANOVA showed that discrimination was significant (Wilks' $\lambda = 0.187$; $F_{24, 779} = 20.0$; $P < 0.001$) and that 77% of the variation was described by the first discriminant function. The first three discriminant functions together accounted for 100% of variation. Overall, of the six call parameters measured, the start frequency, duration and end frequency were the most important for the classification of calls to species (Table 3.4).

Calls of *Myotis brandtii* were the longest of the FM calls in duration (mean 3.1 ms). Calls of *Myotis mystacinus* were similar to those of *Myotis brandtii* in peak frequency (around 48 kHz), bandwidth (around 50 kHz), and start and end frequency (around 88 and 33 kHz), but were of shorter duration (mean 2.2 ms). Calls of both *Myotis brandtii* and *Myotis mystacinus* were frequently misclassified, most often to *Myotis daubentonii* (Table 3.2). Calls of *Myotis nattereri* had short interpulse intervals (mean 77 ms), were very broad band (mean bandwidth 76 kHz) and often swept down to frequencies audible to humans (below 20 kHz). Calls of *Myotis daubentonii* were of relatively long duration (mean 2.9 ms) and also had short interpulse intervals (mean 79 ms). The peak frequency was the lowest of *Myotis* species (mean 46 kHz). Calls of *Plecotus auritus* were of very short duration (about 1.5 ms) and had short interpulse intervals (mean 71 ms). The peak frequency was low (mean 43 kHz), the bandwidth very narrow (32 kHz). This may be attributable to the lower mean start frequency (61 kHz) of calls of *Plecotus auritus* compared with that of other FM bats. *Plecotus auritus* sometimes diverted most of its energy into the second harmonic of its calls, so that the call structure was different to that of other FM calls (Figure 3.2). As only seven individuals of *Myotis bechsteinii* had been recorded, this species could not be included in the discriminant analysis. Calls of *Myotis bechsteinii* were of fairly long duration and very broad band, starting at on average 111 kHz and sweeping down linearly to 34 kHz in about 2.5 ms. This represents the widest bandwidth (mean 77 kHz) of the FM bats, and calls of *Myotis bechsteinii* also had the longest recorded interpulse intervals of FM bats (mean 96 ms).

Most FM calls were linear in frequency modulation, but all FM bats sometimes produced calls which were less steeply frequency-modulated in the centre than at the start and end (see Figure 3.2).

FM/CF calls

When the six parameters were submitted to quadratic discriminant analysis with specified prior probabilities and cross validation, 89% of 250 calls made by *Pipistrellus* and *Nyctalus* species and *Eptesicus serotinus* were reclassified correctly to one of the six species (Table 3.3). Random classification would have been approximately 17% correct. A MANOVA showed that discrimination was significant (Wilks' $\lambda = 0.004$; $F_{30, 958} = 97.0$; $P < 0.001$) and that 92% of the variation was described by the first discriminant function. Table 3.4 shows that, of the six call parameters measured, start frequency, end frequency and centre frequency were the most important for the classification of calls to species. All parameters were important, however.

Calls of *Pipistrellus nathusii* were, on average, of lower peak frequency (39 kHz) and of longer duration (6.1 ms) than those of 45 kHz *Pipistrellus pipistrellus* (46 kHz and 4.8 ms) and 55 kHz *Pipistrellus pipistrellus* (54 kHz and 4.1 ms). There was also a difference in bandwidth; calls of *Pipistrellus nathusii* swept over 13 kHz, while those of 45 kHz and 55 kHz *Pipistrellus pipistrellus* swept over about 30 kHz (see Figure 3.3). In classification, there was very little mixing between the three *Pipistrellus* species and no mixing between *Pipistrellus* species on one hand and *Nyctalus* species and *Eptesicus serotinus* on the other (Table 3.3).

Calls of *Nyctalus leisleri* were intermediate to those of *Nyctalus noctula* and *Eptesicus serotinus* in terms of duration (mean 8 ms), interpulse interval (mean 177 ms), peak frequency (mean 28 ms), start frequency (mean 44 kHz), end frequency (mean 25 kHz), centre frequency (mean 30 kHz) and bandwidth (mean 19 kHz). There was often a change in the degree of frequency-modulation in the central portion of the calls; the first half was more steeply FM than the second half. Calls of *Nyctalus leisleri* were of two types (low frequency and high frequency; extremes are shown in Figure 3.4), but a continuum between types existed and individual calls often could not be classified to a type. Calls of *Nyctalus noctula* were of the longest duration (mean 20 ms) and interpulse interval (mean 336 ms), the lowest peak frequency (mean 20 kHz), and the narrowest bandwidth (mean 7.7 kHz) of those of the three species, and were also of two types (see Figure 3.4). Calls of *Eptesicus serotinus* were of the shortest duration (mean 5.2 ms) and interpulse interval (mean 116 ms), the highest peak frequency (mean 32 kHz) and the largest bandwidth (mean 30 kHz) of those of the three species (see Figure 3.4).

The most common misclassifications in FM/CF calls were between *Nyctalus leisleri* and *Eptesicus serotinus;* ten out of 36 calls of *Nyctalus leisleri* were misclassified

to *Eptesicus serotinus*, and seven out of 55 calls of *Eptesicus serotinus* were misclassified to *Nyctalus leisleri* (Table 3.3).

Discussion

I expect interspecific variation in the echolocation calls used by bats to conform to predictions of scaling with body mass (Barclay & Brigham 1991; Jones 1996a). Thus, compared to small bats, large bats should have echolocation calls of low frequency, high duty cycle and long interpulse interval (Jones 1994). For the species calling at low and intermediate duty cycles recorded for this chapter, mean peak frequency of echolocation call decreased with increasing body size (forearm length) as expected (Figure 3.5). *Rhinolophus* species put most of their energy into the second harmonic, which may explain why they fall above the line representing the other bat species (Figure 3.5). The peak frequencies of echolocation calls made by *Rhinolophus* species decrease with increasing body size (Heller & von Helversen 1989).

Interspecific variation in echolocation call structure and perception technique should also reflect differences in wing morphology and flight and hunting behaviour. For example, bats which hunt by long-range aerial hawking should use low frequencies for the echolocation of distant targets, because high frequencies attenuate more rapidly than low frequencies (Lawrence & Simmons 1982). Bats which glean should use brief calls of low intensity, to avoid overlap between their pulses and echoes of close targets (Neuweiler 1989). The perception techniques used in by the bats recorded for this study are discussed in more detail below.

FM/CF/FM calls

Search phase calls made in the laboratory and in the field by *Rhinolophus ferrumequinum* and *Rhinolophus hipposideros* have been recorded by Vogler & Neuweiler (1983), Ahlén (1988) and Jones & Rayner (1989). These calls were similar in structure to those presented here. Intraspecific variation in echolocation calls has been attributed to flight situation or degree of clutter (Schnitzler 1968; Vogler & Neuweiler 1983) and to age and season (Jones & Ransome 1993) in *Rhinolophus ferrumequinum*, and to age and sex in *Rhinolophus hipposideros* (Jones, Gordon & Nightingale 1992). Both *Rhinolophus* species are very flexible in their hunting behaviour, and variation in echolocation calls occurs in conjunction with this flexibility. For example, calls used in aerial hawking by *Rhinolophus*

ferrumequinum have FM components of greater bandwidth than calls used while searching for prey from perches (Jones & Rayner 1989).

The long FM/CF/FM calls with high duty cycle used by *Rhinolophus* species are suited to the detection of moving prey on a motionless background, by virtue of echoes of the CF component. This perception technique is flutter detection. The echoes of the FM components provide the bat with information about its distance from objects (Simmons, Fenton & O'Farrell 1979).

FM calls

In multivariate discriminant analysis, the lowest level of correct classification was for *Myotis mystacinus* (Table 3.2). For this species, which was most often misclassified as *Myotis daubentonii*, only a small sample size was available. Perhaps if more data could be collected, the overall correct classification rate could be improved. Over 70% of calls made by *Myotis nattereri*, *Myotis daubentonii* and *Plecotus auritus* were classified correctly, and of species in this group, these are by far the most common in Great Britain (Harris *et al.* 1995). Some of the mixing between *Myotis* and *Plecotus* species may have occurred because of variability in several parameters measured from the calls of *Plecotus auritus*. The fundamental or the second harmonic contained most energy and was measured from calls of this species, whereas in calls of *Myotis* species, the fundamental always contained most energy and was measured.

The calls produced by *Myotis* species have been described by Ahlén (1981; *Myotis mystacinus* and *Myotis bechsteinii*), Jones & Rayner (1988) and Kalko & Schnitzler (1989; *Myotis daubentonii*) and in the laboratory by Waters & Jones (1995; *Myotis brandtii* and *Myotis nattereri*). Calls of *Myotis daubentonii* recorded during hunting over water (Jones & Rayner 1988; Kalko & Schnitzler 1989) are of longer duration than those I recorded near roost exits. Konstantinov & Makarov (1981) described calls of *Barbastella barbastellus* which swept up and down in frequency. *Plecotus auritus* produce very quiet calls and sometimes divert much of the energy into the second harmonic (Ahlén 1981; Waters & Jones 1995). Calls of *Plecotus austriacus* are similar to those of *Plecotus auritus* (Ahlén 1990). Ahlén (1981) describes a second call type made by *Plecotus auritus* which may be used for echolocation or communication. Calls of this type, produced at rates of around five per second, are intense and long (*circa* 7 ms), and sweep down in frequency from 42 to 12 kHz. With the exception of this call type and the duration of calls of *Myotis daubentonii*, call parameters from the literature are similar to those described here. However, samples of calls recorded near roost exits are likely to be biased towards the

types of calls generally used near clutter. These calls are of shorter duration and wider bandwidth than those used by bats flying in open spaces.

Broad-band FM calls are suitable for prey detection in dense clutter and over water surfaces, as the bat can build up a detailed acoustic image of background and target from the echoes of such calls. Very short-duration broad-band FM calls such as those used by *Myotis bechsteinii* and *Myotis nattereri*, and short-duration, low-intensity multi-harmonic calls like those used by *Plecotus auritus*, are suitable for the detection of insects on surfaces, which can be caught by gleaning (Simmons, Fenton & O'Farrell 1979, Neuweiler 1989). *Plecotus auritus* also hunts by passive listening (Anderson & Racey 1991).

The calls of *Myotis bechsteinii*, *Barbastella barbastellus* and *Plecotus austriacus* could not be included in the discriminant analysis. These species, along with *Rhinolophus ferrumequinum*, are the rarest in Great Britain, with estimated populations of 5000 individuals or less (Harris *et al.* 1995; see Table 1.1). When seven calls made by seven individuals of *Myotis bechsteinii* were submitted to the discriminant function, they were assigned to *Myotis brandtii* (three calls), *Myotis mystacinus* (one call), and *Myotis nattereri* (three calls). When three calls made by one individual of *Barbastella barbastellus* were submitted, they were assigned to *Myotis daubentonii.*

In conclusion, FM bats, such as *Myotis* species, use calls which are extremely similar in structure. These bat species cannot be identified from their calls with certainty, though a good degree of confidence in species identification can be achieved by multivariate analysis of call parameters.

FM/CF calls

The calls of *Pipistrellus pipistrellus* described in this chapter are of shorter duration than those in the literature, while calls of *Pipistrellus nathusii* seem to have similar time and frequency parameters in all studies (Jones & van Parijs 1993; Kalko & Schnitzler 1993; Kalko 1995). The calls of *Nyctalus leisleri* have been described previously (Zingg 1988; Waters, Rydell & Jones 1995), as have those of *Nyctalus noctula* (Vogler & Neuweiler 1983; Zbinden 1989) and *Eptesicus serotinus* (Tupinier, Biraud & Chiollaz 1980-1981; Miller & Degn 1981). Call parameters presented here are similar to those described in the literature, but probably represent a sample slightly biased towards the short, broad-band calls with reduced CF component, used by bats flying near clutter. Calls of *Nyctalus leisleri* and *Nyctalus noctula* are often of two types, high and low frequency, which are sometimes alternated during flight (Zbinden 1989; Waters, Rydell & Jones 1995). For this

study, both types were analysed together, as the distinction between types was not always clear (Figure 3.4).

In the FM/CF calls used by *Pipistrellus* and *Nyctalus* species and by *Eptesicus serotinus*, the echo of the FM component can be used to form an acoustic image of the background, while the echo of the CF component can be used to search for prey and perhaps in flutter detection. FM/CF calls are suitable for use in open environments with some obstacles (Simmons, Fenton & O'Farrell 1979), and can be adapted according to the proximity of obstacles as described above. FM/CF calls of lower frequencies attenuate less rapidly than those of higher frequency (Lawrence & Simmons 1982) and are therefore more suitable for use in very open spaces (Fenton 1990). Thus, I expect *Nyctalus* species and *Eptesicus serotinus* to forage more commonly in open spaces than *Pipistrellus* species.

Conclusion

Intraspecific variation in echolocation calls is attributed to hunting behaviour and habitat (Kalko & Schnitzler 1993; Obrist 1995), and to individual identity (Masters, Raver & Kazial 1995). Characteristics of echolocation calls also scale across species with body mass (Jones 1996b) and vary intraspecifically with sex and age (Jones, Gordon & Nightingale 1992; Jones & Kokurewicz 1994; Masters, Raver & Kazial 1995). The calls included here probably represent a sample biased towards short duration, wide bandwidth calls used by bats flying near clutter. This is because most of the recordings were made outside roosts. The calls used by bats flying in clutter converge in structure across species, and the method described here could almost certainly be improved if more bats could be recorded under different conditions. To include more of the variation in echolocation calls produced by bats in natural conditions, more recordings of bats flying at high altitude away from clutter should be added to the database. This would probably require bats to be marked with chemiluminescent tags (Buchler 1976; Kunz 1988) and recorded on release.

However, when calls of unknown bats are recorded in the field; for example for the survey in Chapter 4, they can be analysed in the way described here and classified to species level. This method is suitable for the assessment of habitat requirements of British bat species, and could be adapted for use in other geographical areas. Because of the level of uncertainty inherent in this and other methods of the identification of bats from echolocation calls for several species, I do not recommend these methods for the collection of distributional records (as done by Hooper 1981 and Jüdes 1987a). In surveys of habitat use by bats, when a quantified degree of uncertainty is acceptable, I recommend that tapes

of echolocation calls are analysed blind. This way, the researcher's subjective expectation of the bats to be found in a given habitat cannot influence counts of bat passes.

Due to differences in their structure and intensity, the calls of British species of bats have different degrees of acoustical apparency (Waters & Jones 1995) and are subject to different levels of atmospheric attenuation (Lawrence & Simmons 1982). Therefore, in surveys of habitat use, levels of bat activity quantified from identified calls cannot be compared across species. However, levels of the activity of each species can be related to different habitat types independently, and it is possible to describe the habitat requirements of each species of bat (Chapter 4).

Table 3.1 (next page) Time and frequency parameters of echolocation calls made by all British bat species except *Plecotus austriacus*. One call per bat was analysed. The table shows **mean** ± standard deviation (minimum-maximum) of parameters for the sample sizes of bats given (*n* bats = number of bats; *n* locs = number of locations or roosts). S = call structure; CF = constant frequency, FM = frequency modulated. For definitions of parameters, see 'Methods' above.

Bat species	S	*n* bats	*n* locs	Duration (ms)	Interpulse interval (ms)	Peak frequency (kHz)	Start frequency (kHz)	End frequency (kHz)	Centre frequency (kHz)
R. ferrumequinum	FM/CF/FM	21	3	**49.4** ± 13.3 (26.7 - 69.1)	**83.0** ± 18.9 (33.8 - 106)	**82.3** ± 1.05 (80.8 - 84.4)	**69.3** ± 3.15 (64.4 - 77.6)	**70.3** ± 5.25 (62.8 - 80.8)	**82.1** ± 1.62 (80.0 - 84.4)
R. hipposideros	FM/CF/FM	24	1	**45.7** ± 8.98 (23.9 - 63.9)	**82.4** ± 12.3 (54.4 - 118)	**109** ± 2.13 (106 - 113)	**98.2** ± 6.09 (85.6 - 108)	**96.1** ± 8.47 (84.0 - 110)	**109** ± 2.18 (106 - 112)
M. brandtii	FM	42	2	**3.06** ± 0.83 (1.50 - 5.00)	**88.0** ± 18.3 (56.9 - 168)	**47.9** ± 8.29 (38.0 - 78.4)	**85.5** ± 13.3 (59.2 - 123)	**33.7** ± 3.78 (26.8 - 41.6)	**54.9** ± 6.06 (44.8 - 70.4)
M. mystacinus	FM	25	5	**2.23** ± 0.92 (0.30 - 4.00)	**87.8** ± 23.8 (47.5 - 140)	**47.5** ± 5.91 (38.8 - 65.2)	**80.3** ± 12.1 (56.0 - 102)	**32.2** ± 3.35 (26.8 - 38.8)	**52.4** ± 4.79 (44.0 - 61.6)
M. bechsteinii	FM	7	2	**2.54** ± 0.53 (1.60 - 3.00)	**96.4** ± 13.1 (79.4 - 120)	**51.0** ± 3.13 (45.6 - 55.2)	**111** ± 22.3 (65.6 - 131)	**33.8** ± 3.90 (28.4 - 38.8)	**68.8** ± 10.1 (51.2 - 83.2)
M. nattereri	FM	67	5	**2.29** ±1.10 (0.50 - 5.30)	**76.8** ± 24.8 (24.4 - 150)	**51.2** ± 11.3 (26.8 - 81.2)	**98.5** ± 19.6 (57.2 - 146)	**22.5** ± 5.10 (14.8 - 47.2)	**57.7** ± 11.9 (32.8 - 89.6)
M. daubentonii	FM	61	6	**2.91** ± 0.95 (1.30 - 5.80)	**78.6** ± 22.6 (44.4 - 171)	**46.2** ± 4.48 (30.4 - 54.8)	**81.4** ± 13.1 (49.2 - 110)	**29.4** ± 3.74 (22.4 - 40.4)	**51.7** ± 5.39 (35.2 - 64.0)
B. barbastellus	FM ?	1	1	4.40	63.8	36.8	46.0	28.4	38.4
P. auritus	FM	38	5	**1.48** ± 0.60 (0.50 - 2.50)	**71.3** ± 25.0 (20.0 - 140)	**43.3** ± 9.16 (30.4 - 74.8)	**60.5** ± 15.9 (42.8 - 100)	**28.5** ± 5.41 (20.4 - 43.2)	**41.6** ± 10.2 (28.8 - 64.0)
P. nathusii	FM/CF	14	4	**6.12** ± 1.24 (3.00 - 7.70)	**134** ± 55.9 (87.5 - 246)	**39.3** ± 1.00 (37.2 - 40.8)	**49.8** ± 6.76 (40.0 - 66.8)	**36.7** ± 1.02 (35.2 - 38.4)	**39.7** ± 1.98 (38.4 - 44.8)
45 kHz ***P. pipistrellus***	FM/CF	60	3	**4.81** ± 1.25 (2.60-7.30)	**98.2** ± 32.1 (54.4 - 185)	**46.0** ± 1.81 (41.6 - 50.8)	**71.3** ± 14.0 (53.6 - 119)	**43.3**± 1.78 (38.8 - 48.4)	**46.8** ± 2.30 (41.6 - 51.2)
55 kHz ***P. pipistrellus***	FM/CF	59	3	**4.10** ± 0.88 (2.20 - 6.60)	**95.2** ± 27.5 (58.1 - 198)	**53.8** ± 1.70 (49.2 - 57.6)	**81.9** ± 9.37 (65.2 - 114)	**50.6** ± 1.91 (45.2 - 54.4)	**54.9** ± 2.14 (51.2 - 60.8)
N. leisleri	FM/CF	36	3	**8.01** ± 2.66 (4.10 - 15.0)	**177** ± 71.6 (86.3 - 338)	**28.2** ± 3.00 (21.6 - 34.8)	**44.0** ± 12.6 (24.8 - 80.0)	**25.3** ± 2.33 (19.2 - 29.2)	**29.8** ± 4.07 (21.6 - 38.4)
N. noctula	FM/CF	26	3	**19.6** ± 4.38 (10.9 - 33.5)	**336** ± 138 (140 - 900)	**20.3** ± 2.01 (16.8 - 26.0)	**25.9** ± 7.16 (18.8 - 52.8)	**18.2** ± 2.12 (15.2 - 24.4)	**20.9** ± 2.70 (16.0 - 28.8)
E. serotinus	FM/CF	55	2	**5.22** ± 2.08 (1.60 - 11.7)	**116** ± 26.2 (63.8 - 155)	**32.3** ± 3.67 (25.6 - 42.4)	**57.4** ± 7.96 (39.2 - 78.0)	**27.7** ± 1.85 (22.4 - 32.0)	**36.0** ± 3.41 (28.0 - 44.8)

Table 3.2 Summary of classification of FM bats by quadratic discriminant analysis of call parameters (*M. b.* = *Myotis brandtii*, *M. m.* = *Myotis mystacinus*, *M. n.* = *Myotis nattereri*, *M. d.* = *Myotis daubentonii* and *P. a.*= *Plecotus auritus*). Overall, 67% of 233 calls were reclassified correctly.

	True species:				
Classified as:	***M. b.***	***M. m.***	***M. n.***	***M. d.***	***P. a.***
M. b.	23	3	1	3	4
M. m.	2	3	1	6	0
M. n.	2	1	58	1	3
M. d.	14	13	3	46	4
P. a.	1	5	3	5	27
n	42	25	67	61	38
n correct	23	3	58	46	27
% correct	55	12	87	75	71

Table 3.3 Summary of classification of FM/CF bats by quadratic discriminant analysis of call parameters (*P. n.* = *Pipistrellus nathusii*, *P. p. (45)* = 45 kHz *Pipistrellus pipistrellus*, *P. p. (55)* = 55 kHz *Pipistrellus pipistrellus*, *N. l.* = *Nyctalus leisleri*, *N. n.* = *Nyctalus noctula* and *E. s.* = *Eptesicus serotinus*). Overall, 89% of 250 calls were reclassified correctly.

	True species:					
Classified as:	***P. n.***	***P.p. (45)***	***P. p. (55)***	***N. l.***	***N. n.***	***E. s.***
P. n.	11	0	0	0	0	0
P. p. (45)	3	58	2	0	0	0
P. p. (55)	0	2	57	0	0	0
N. l.	0	0	0	25	1	0
N. n.	0	0	0	1	24	7
E. s.	0	0	0	10	1	48
n	14	60	59	36	26	55
n correct	11	58	57	25	24	48
% correct	79	97	97	69	92	87

Table 3.4 Communalities (overall importance) of call parameters used in the discriminant analysis, calculated as sum of squares of cross correlations by rows.

Call parameter	FM bats	FM/CF bats
Duration	0.937	0.997
Interpulse interval	0.482	0.987
Peak frequency	0.495	0.991
Start frequency	0.951	1.000
End frequency	0.928	1.000
Centre frequency	0.757	1.000

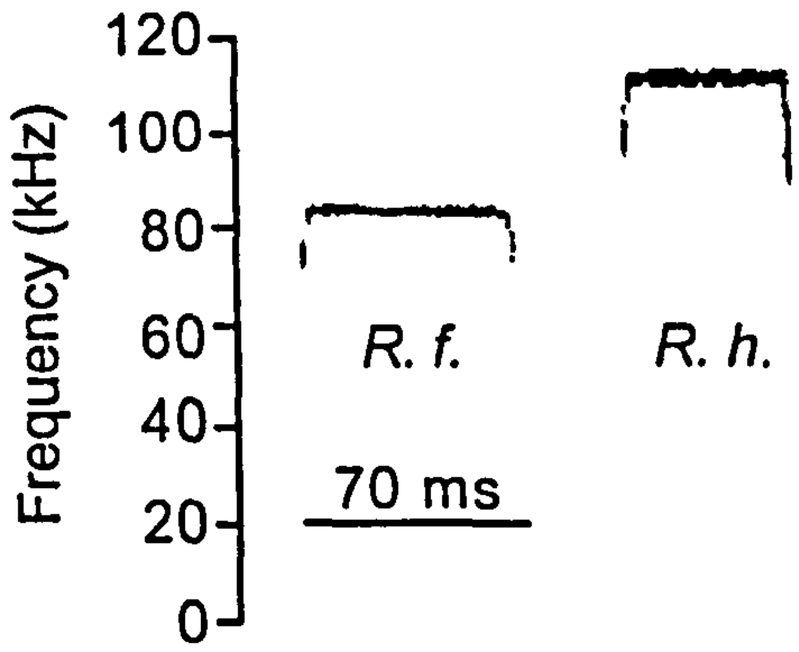


Figure 3.1 Sonagrams of echolocation calls by the FM/CF/FM bats *Rhinolophus ferrumequinum* (*R. f.*) and *Rhinolophus hipposideros* (*R. h.*).

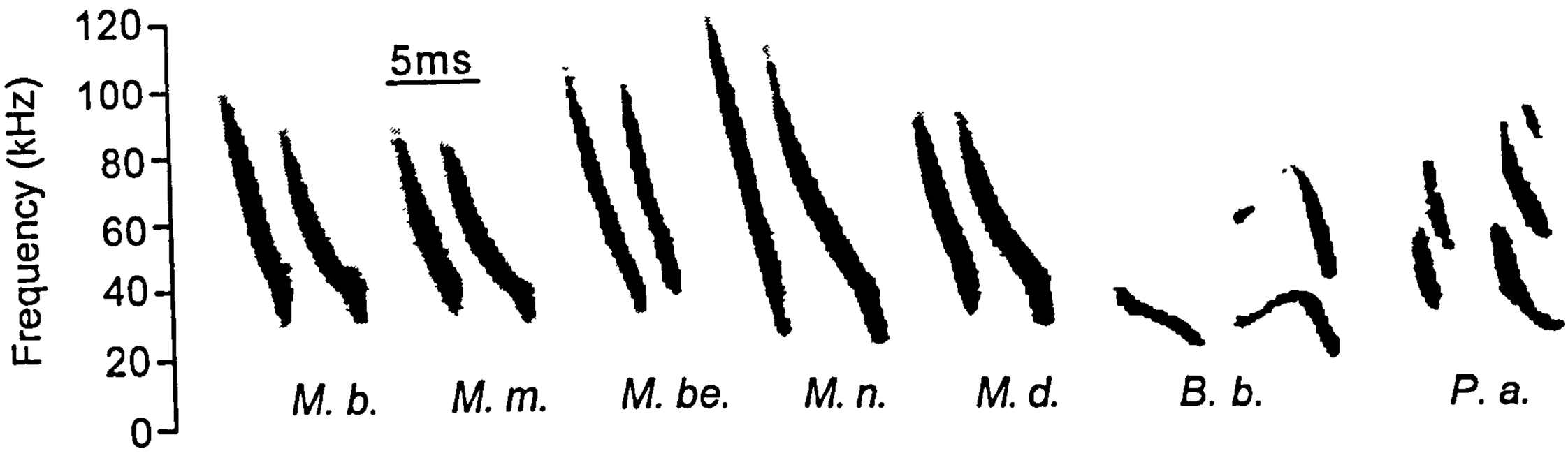


Figure 3.2 Sonagrams of two echolocation calls by each of the FM bats *Myotis brandtii* (*M. b.*), *Myotis mystacinus* (*M. m.*), *Myotis bechsteinii* (*M. be.*), *Myotis nattereri* (*M. n.*), *Myotis daubentonii* (*M. d.*) and *Plecotus auritus* (*P. a.*). Calls of *Barbastella barbastellus* (*B. b.*) are also shown. Two calls of each species are included, in order to show some intraspecific variation.

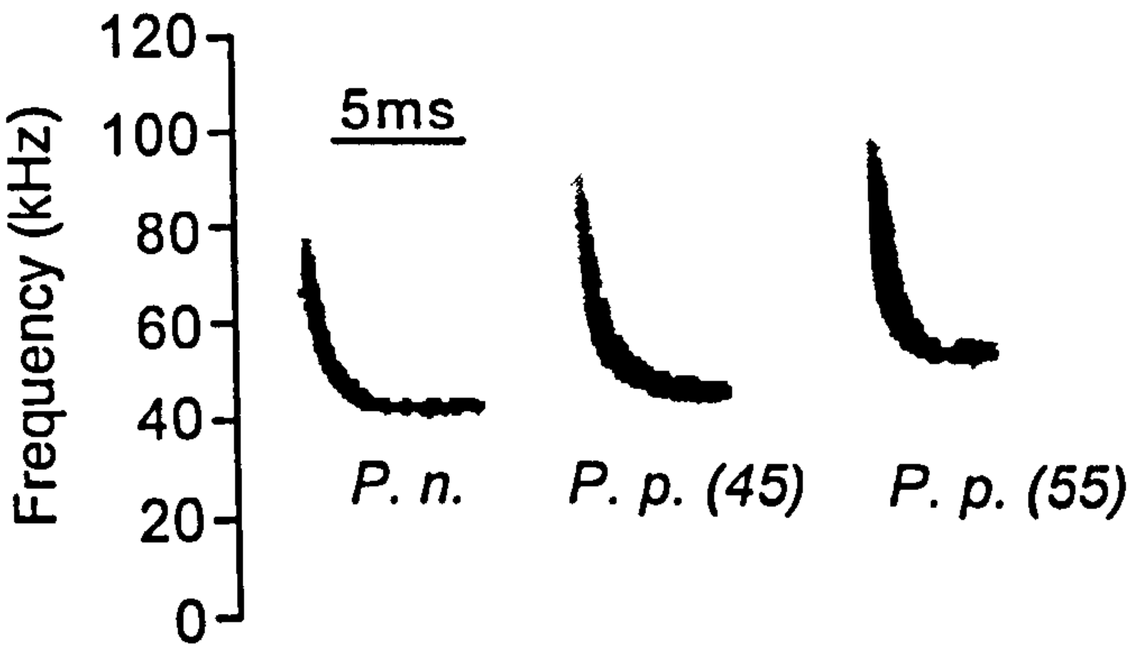


Figure 3.3 Sonagrams of echolocation calls by the FM/CF bats *Pipistrellus nathusii* (*P. n.*), 45 kHz *Pipistrellus pipistrellus* (*P. p. (45)*) and 55 kHz *Pipistrellus pipistrellus* (*P. p. (55)*).

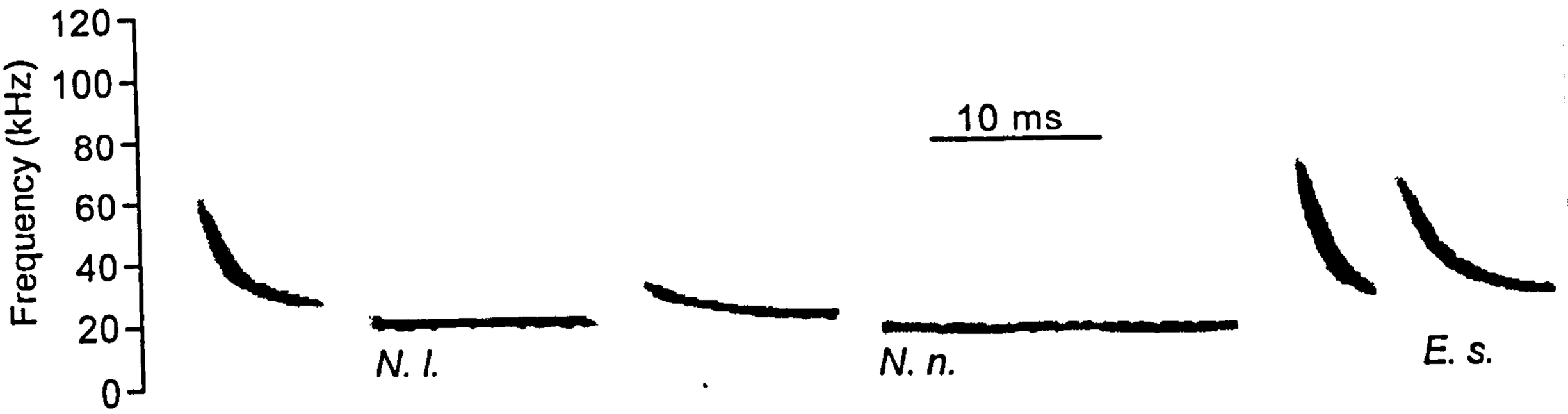


Figure 3.4 Sonagrams of two echolocation calls by each of the FM/CF bats *Nyctalus leisleri* (*N. l.*), *Nyctalus noctula* (*N. n.*) and *Eptesicus serotinus* (*E. s.*). For each species, the two calls represent extremes of high and low frequency, which are sometimes alternated by *Nyctalus leisleri* and *Nyctalus noctula*.

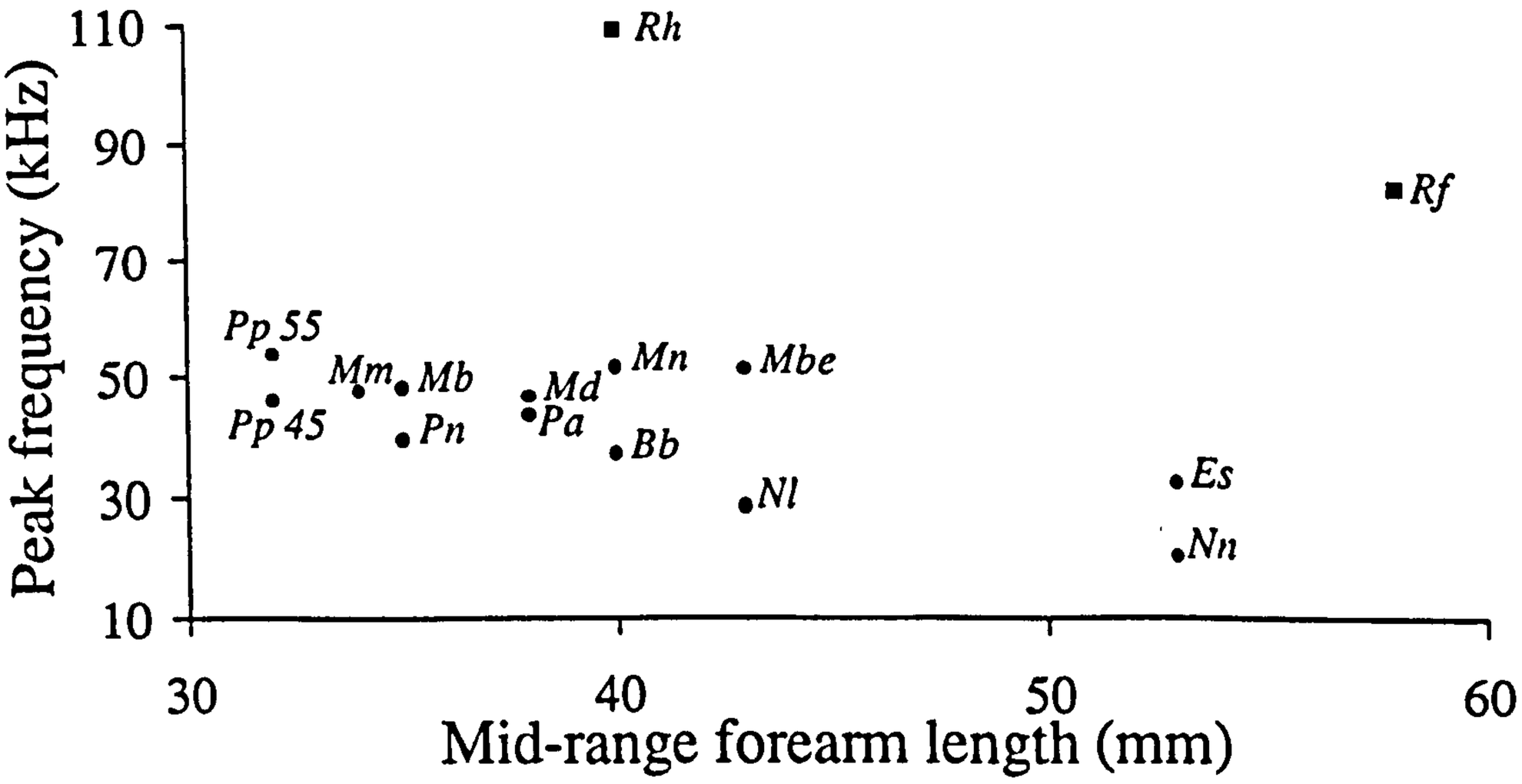


Figure 3.5 The relationship between mean peak frequency of echolocation calls (kHz) and mid-range forearm length (mm; Schober & Grimmberger 1987) for 15 British species of bats. Bats which always put most energy in the second harmonic of their calls (■) fall above other bats (●). Abbreviations are as in Figures 3.1-3.4.

FOUR

Habitat use by bats assessed by means of a broad-band acoustic method

A paper based on this chapter has been submitted to *Journal of Applied Ecology*.

Habitat use by bats assessed by means of a broad-band acoustic method

Summary

Bat foraging activity was quantified, by using the broad-band acoustic method described in Chapter 3, on transects in ten land use types in south-west England. From broad-band recordings of echolocation calls, 83% of bat passes could be identified to species level with quantified degrees of certainty. The remaining 17% could be identified to species group. Total bat activity was positively correlated with air temperature, and, once adjusted for temperature, was significantly higher over rivers and lakes than over other land use types. Rhinolophus *species, though rarely recorded, foraged mostly in pasture and woodlands.* Myotis *species and* Plecotus auritus *were recorded in many land use types, but never in villages. Rivers and lakes supported high levels of activity of these species. Bats classified as 45 kHz* Pipistrellus pipistrellus *fed in many habitats, while 55 kHz* Pipistrellus pipistrellus *fed mainly over rivers and lakes. Bats classified as* Nyctalus noctula, Nyctalus leisleri *and* Eptesicus serotinus *were most active in open habitats and over rivers and lakes. Total bat activity was equally high in woodland interiors and along woodland edges, but bats were relatively more active in sheltered sections of transects than in exposed sections. Plans for land management should take into account the habitat needs of bats. For most species of bat found in Britain, the conservation of rivers and lakes is of primary importance.*

Introduction

Bat detector studies generally confirm predictions, derived from wing morphology and echolocation call structure, of resource partitioning through bats' hunting behaviour and habitat use (e.g. Furlonger, Dewar & Fenton 1987; McAney & Fairley 1988; Moeschler & Blant 1990). Some dietary and habitat use studies suggest that bats are, to a certain extent, opportunistic in their foraging habits (e.g. Fenton & Thomas 1980; Swift, Racey & Avery 1985). The large-scale National Bat Habitat Survey in the United Kingdom (Walsh, Harris & Hutson 1995) made use of narrow-band tuned bat detectors, so that results mainly reflect the combined distribution of *Pipistrellus pipistrellus* and *Myotis* species (Ahlén 1990; Zingg 1990). The Bat Habitat Survey reveals nothing about the habitat preferences of different species of bats, but does show which habitats support high numbers of foraging bats (Walsh, Harris & Hutson 1995).

Although the conservation of roost sites is important for the maintenance of populations of bats (Kunz 1982), after closure of roosts individual bats are loyal to foraging sites and find new roosts (Brigham & Fenton 1986). This suggests that the conservation of foraging habitats is important. Populations of bats are likely to be limited mainly by the availability of resources, and changes in foraging habitats which lead to changes in insect densities are expected to lead to changes in bat populations (Findley 1993; Gerell & Lundberg 1993; see Chapter 1). However, under current legislation in the United Kingdom, bat roosts are afforded far better protection than foraging sites (Wildlife and Countryside Act 1981; Conservation (Natural Habitats 2c) Regulations 1994).

The aim of this study was to quantify the relative importance of sites in ten common land use types for foraging bats. With a view to bat conservation and land management, I hoped to identify important foraging sites for each species of bat found in Great Britain.

Methods

Study sites

I aimed to compare levels of bat activity in different land use types in south-west England, while controlling for differences in activity due to land class (as defined by the Institute of Terrestrial Ecology's land classification system; Bunce & Heal 1984). The 30 study sites were therefore chosen in the undulating lowland pastoral land classes one, five and six, the most common group of land classes in south-west England. Land class has a significant effect on bat activity, but no significant difference in activity was found in the land classes used in this study (Walsh, Harris & Hutson 1995).

Within these land classes, ten common land use types were chosen (Pinches & Lister 1988; Nature Conservancy Council 1990). Three replicate sites, at least 5 km from each other, were found in each of the ten land use types and each site was visited on three nights between 25 April and 28 October 1993. One visit fell in each of the three main periods of bat activity, called seasons: prelactation (25 April-11 June), lactation (24 June-9 August), and postlactation (13 September-28 October). These dates hold for most British species of bats (Corbet & Harris 1991). Sites were visited in random order within each season. Table 4.1 shows the land use types and sites.

Sites were large enough for a 2 km transect, called the main transect, to be planned in each. Main transects usually ran entirely within the land use type. If this was impossible, a break of less than five minutes without sampling was included. Main transects in land use types one to six were subdivided into sheltered and exposed sections, sheltered sections being those within 10 m of trees, hedges, or buildings. In land use type seven, villages, lit subdivisions of main transects were those within 10 m of street lamps. In land use types eight, nine, and ten, main woodland transects were on paths or off paths, and a second 0.5 km transect, called the edge transect, was walked along the edge of the woodland after the main transect had been completed.

Sites were visited in daylight for habitat assessment and transect planning, and main transects and edge transects were drawn onto 1:2500 Ordnance Survey maps.

Sound recording

Two S-25 bat detectors were linked to a PUSP and a Professional Walkman exactly as described in Chapter 3 (page 57). The output from frequency division was used to count

bats passes (see page 18). The PUSP was activated each time a bat was heard on the frequency division channel of the Walkman. A recording of bat calls was made on each transect on a 90-minute metal tape (see page 57).

Sampling technique

Each main transect was walked for 45 minutes, starting 30 minutes after sunset. Because walking speed on transects affects counts of bat passes (Walsh, Harris & Hutson 1995), a fixed walking speed of 2.7 km/h was adhered to on both main and edge transects.

The bat detectors were mounted on the PUSP and held at elbow height aimed to the left. Before starting and after finishing the main transects, the air temperature at waist height was measured and the wind speed was estimated (Beaufort scale). The means of values before and after sampling are referred to as the temperature and wind speed for each sample. No field research was undertaken in heavy rain, as the recording equipment can be damaged by moisture. Each night, the percentage of the moon face illuminated was recorded (Whitaker 1993), and the percentage cloud cover was estimated at the start of each main transect. The subdivision of the transect was recorded onto a micro-cassette recorder (Olympus, London; Pearlcorder S803) in relation to the tape counter on the Walkman. A map was carried for navigation.

Sound analysis

A Sonagraph (see page 58 for details) was used to analyse the recordings. Numbers of bat passes were counted on the frequency-division channel. Parameters taken from time-expanded calls were used for bat species identification according to Jones & van Parijs (1993) for 45 kHz and 55 kHz *Pipistrellus pipistrellus* and the method described in Chapter 3 for unidentified *Pipistrellus pipistrellus* (peak frequency 49-52 kHz; Jones & van Parijs 1993) and other species. No prior probabilities were entered into the models. Calls of *Myotis bechsteinii*, *Barbastella barbastellus* and *Plecotus austriacus* are not included in the multivariate model (Chapter 3). This means that the calls of these rare species, had they been recorded in this study, would have been misclassified. However, they would probably have been attributed to the *Myotis* and *Plecotus* species group, because of the structure of their calls (Chapter 3).

For each main transect the total number of bat passes, the number of bat passes attributed to each species, and the subdivision of the land use type in which passes occurred was recorded. The fact that the sites were being used for foraging could be confirmed because most vespertilionid bats produce distinctive terminal phase

echolocation calls or buzzes while attempting prey capture (Griffin, Webster & Michael 1960). Overall, terminal buzzes were heard in 7% of bat passes on main transects (range 0-30%). Counts of bat passes were therefore used as a measure of foraging activity. Furlonger, Dewar & Fenton (1987) and Walsh & Harris (1996) used a similar approach and found that around 10% and 20% of passes respectively contained terminal buzzes. The feeding activity of 45 kHz and 55 kHz *Pipistrellus pipistrellus* was also expressed as the ratio of terminal buzzes to passes. This ratio is called the buzz ratio, a buzz ratio of one indicating that equal numbers of passes and buzzes were heard, or that on average every pass contained a buzz. The buzz ratio is a measure of foraging effort per unit of flight activity. Buzz ratios were not calculated for other species, as numbers of buzzes recorded were low.

Social calls / song-flight calls produced by 45 kHz and 55 kHz *Pipistrellus pipistrellus* were counted. The two call types could not be distinguished from one another in this study, but it was possible to assign each call to one of the sibling species, as they are produced in conjunction with echolocation calls.

In exploratory data analysis it was apparent that, of the measured environmental parameters, temperature alone affected bat activity. Wind speed, moon phase and cloud cover had no discernible effect on bat activity, and were therefore omitted from further analyses. For the analysis of counts of bat passes on main transects, separate analyses of covariance (ANCOVAs) were carried out on species for which transformed counts of passes conformed to the assumptions of ANCOVA (Zar 1984). Site was nested within land use type, season was a crossed factor and temperature was the covariate. Non-significant interaction terms were omitted from the model one by one, using the model simplification procedure advocated by Aitkin *et al.* (1989), and only the results from the final resulting ANCOVA are given here. Adjusted means, representing effects independent of the covariate, were compared long-hand using the Bryant-Paulson-Tukey test (Day & Quinn 1989).

Counts of social / song-flight calls, bat passes on edge transects and bat passes on main transect subdivisions were analysed with paired tests. Where data were normally distributed with homogeneous variances (Altman 1991), and the differences between pairs of counts were normally distributed, the paired *t*-test was used. The Wilcoxon signed rank test requires the differences between pairs in the sample to be symmetrically distributed (Altman 1991). The sign test was used as an alternative to the Wilcoxon signed rank test when the distribution of differences did not meet this requirement.

Results

In all main transects (67 hours and 30 minutes of sampling), a total of 5519 bat passes and 391 terminal buzzes were counted. 278 of the terminal buzzes were produced by 45 kHz and 55 kHz *Pipistrellus pipistrellus*. 4568 of the passes were identified to species level (Table 4.2). The remaining 951 were classified as unidentified *Myotis* or *Plecotus* species (427 passes) or as unidentified *Nyctalus* species or *Eptesicus serotinus* (524 passes). The calls in these passes were of such low intensity that the parameters needed for multivariate analysis could not be measured from them. Overall, a median of 22 bat passes was counted on the 2-km main transects (range 0-483).

Factors affecting total bat activity

Of the measured environmental factors, temperature alone affected total bat activity (see 'Methods' above). In the final ANCOVA on log transformed bat passes, land use type, site and temperature each had a significant effect on bat activity. No interaction terms remained in the model (Table 4.3). The adjusted means of counts of bat passes for each land use type are shown in Figure 4.1. Total bat activity was significantly higher over rivers and lakes than in other land use types, and in all, 70% of bat passes were recorded over rivers and lakes.

Factors affecting the activity of Rhinolophus *species*

Eight passes of *Rhinolophus ferrumequinum* were recorded on main transects; two over unimproved grassland, two over improved cattle pasture, one in a village, two in ancient semi-natural woodland and one in a conifer plantation (Table 4.4).

Thirteen passes of *Rhinolophus hipposideros* were recorded on main transects; two in improved cattle pasture and 11 in woodlands (Table 4.4).

Factors affecting the activity of Myotis *and* Plecotus *species*

Of the 112 passes which were attributed to *Myotis brandtii*, 65 (58%) were recorded over rivers and lakes, 16 over grassland and 30 in woodlands (Table 4.4). Overall, 33 passes were attributed to *Myotis mystacinus*, and of these, 17 (52%) were recorded over rivers and lakes, five in grassland and ten in woodlands. Of the 31 passes attributed to *Myotis nattereri*, 18 (58%) were recorded over rivers and lakes. Of the 276 passes classified as

Myotis daubentonii, 243 (88%) were recorded over rivers and lakes, 12 in grassland, two in arable land and 19 in woodlands. In spite of the large numbers of records of *Myotis daubentonii*, counts of passes attributed to this species could not be transformed to conform to the assumptions of ANCOVA. The 17 passes attributed to *Plecotus auritus* were recorded in eight of the ten land use types. Nine passes were counted in woodlands. None of these five species was ever recorded in a village (Table 4.4).

In the final ANCOVA on log transformed counts of total *Myotis* and *Plecotus* species passes, land use type and site had significant effects. The interaction terms land use type and season, and land use type and temperature, remained in the model and were significant (Table 4.5). The activity of *Myotis* and *Plecotus* species over rivers and lakes was significantly higher than over other land use types, although unimproved grassland, improved cattle pasture, ancient semi-natural woodland and mixed plantations also supported high levels of activity (Figure 4.2).

Factors affecting the activity of Pipistrellus *species*

All 14 passes attributed to *Pipistrellus nathusii* were recorded over rivers and lakes. Eleven of the passes were recorded at Chew Valley Lake, in lactation and postlactation (Table 4.4).

In the final ANCOVA on log transformed counts of passes attributed to 45 kHz *Pipistrellus pipistrellus*, land use type, and to a lesser extent temperature, were found to have significant effects. No interaction terms remained in the model (Table 4.6). In the final ANCOVA on square roots of log transformed 45 kHz *Pipistrellus pipistrellus* buzz ratios, none of the effects or interaction terms was significant (Table 4.6). Figure 4.3 shows the adjusted means of counts of 45 kHz *Pipistrellus pipistrellus* passes (a) and buzz ratios (b) for each land use type. There is no significant difference in activity over rivers and lakes, unimproved grassland, improved cattle pasture, and in conifer plantations and mixed plantations. Generally, individuals of 45 kHz *Pipistrellus pipistrellus* are active and widespread in all land use types (Figure 4.3a), and buzz ratios are evenly distributed over seasons and land use types (Figure 4.3b).

In the final ANCOVA on log transformed counts of passes attributed to 55 kHz *Pipistrellus pipistrellus*, only land use type had a significant effect (Table 4.7). In the final ANCOVA on square roots of log transformed 55 kHz *Pipistrellus pipistrellus* buzz ratios, significant effects of land use type and site were found. No interaction terms remained in either model (Table 4.7). Figure 4.4 shows the adjusted means of counts of 55 kHz *Pipistrellus pipistrellus* passes (a) and buzz ratios (b) for each land use type. 55 kHz

Pipistrellus pipistrellus activity was significantly higher over rivers and lakes than in other land use types (Figure 4.4a). Buzz ratios of 55 kHz *Pipistrellus pipistrellus* were significantly different in different land use types (Figure 4.4b).

Factors affecting the activity of Nyctalus *species and* Eptesicus serotinus

In the final ANCOVA on square roots of log transformed counts of passes attributed to *Nyctalus leisleri*, only land use type had a significant effect. No interaction terms remained in the model (Table 4.8). The activity of *Nyctalus leisleri* was significantly higher near lakes, and over rivers and improved pasture than in other land use types (including rivers and improved pasture) (Figure 4.5).

In the final ANCOVA on square roots of log transformed counts of passes attributed to *Nyctalus noctula*, only land use type had a significant effect. No interaction terms remained in the model (Table 4.9). The activity of *Nyctalus noctula* was significantly higher near lakes and over improved pasture than in other land use types, although no significant difference was found between activity levels over improved pasture, rivers, unimproved grassland, amenity grassland, arable land and villages (Figure 4.6).

The 37 passes attributed to *Eptesicus serotinus* were recorded in eight of the ten land use types. 19 passes (51%) were recorded over rivers and lakes, 12 in grassland (of which seven in improved cattle pasture), four in arable land, one in a village and one in an ancient semi-natural woodland (Table 4.4).

Woodland edges

To investigate the use of woodland edges by foraging bats, regardless of type of wood, season, or temperature, the total number of bat passes counted on the last 0.5 km of the main woodland transect was compared to the number counted on the 0.5 km woodland edge transect. These two counts were treated as paired samples and the resulting paired *t*-test was not significant ($n = 27$; $t = 0.18$). Overall, bats were equally active inside woodlands (on and off paths) and on woodland edges. An equivalent non-parametric test was done for each bat species group. For *Myotis* and *Plecotus* species, and separately for *Pipistrellus* species, Wilcoxon signed rank tests showed that there was no significant difference between levels of activity inside woodlands and along woodland edges ($Z =$

130.0 for *Myotis* and *Plecotus* species; $Z = 98.0$ for *Pipistrellus* species; $n = 27$ for both tests). For *Nyctalus* species and *Eptesicus serotinus*, a sign test gave the same result.

Main transect subdivisions

To quantify the use of the subdivisions of main transects, their availability on transects was first quantified, using maps and data from the micro-cassette recorder. The availability of a subdivision expressed as a proportion of main transect length was compared to the proportion of bat passes (all species) found on that subdivision, using Wilcoxon signed rank tests. This was done in each group of land use types with the same subdivisions, i.e. rivers, lakes, unimproved grassland, amenity grassland, improved cattle pasture and arable land had exposed and sheltered subdivisions; ancient semi-natural woodland, conifer plantations and mixed plantations had on path and off path subdivisions (see Table 4.1). In these tests, records for sites were pooled across seasons. Sheltered transect subdivisions were found to support higher levels of total bat activity than exposed sections (Wilcoxon signed rank test, $n = 54$; $Z = 93.5$; $P < 0.05$), but there was no significant difference between the proportion of transects on woodland paths and the proportion of bat passes recorded from on path transect subdivisions (Wilcoxon signed rank test, $n = 27$; $Z = 0$). Main transects in villages had lit and unlit subdivisions, but statistical evaluation of the distribution of bat passes in relation to these was not possible, as there were only three village sites. Overall, 80% of all main transects in villages was lit, and 71% of bat passes recorded from villages were in lit subdivisions of transects.

Social / song-flight calls

Social / song-flight calls were produced at overall mean rates of 0.33 calls per main transect by 45 kHz *Pipistrellus pipistrellus* and 1.04 calls per main transect by 55 *Pipistrellus pipistrellus*. A paired *t*-test showed the difference in log transformed counts of calls on transects to be significantly different between the sibling species ($n = 90$; t=-2.07; P<0.05). Counts of social / song-flight calls did not conform to the assumptions of ANCOVA, so no further statistical analysis was carried out, but the calls appeared to have been recorded in similar numbers in all seasons and in all land use types.

Discussion

Factors affecting bat activity

Air temperature affects insect distribution (Williams 1961; Richards 1989). The foraging activity of bats relates to insect density (Racey & Swift 1985; but see also Ekman & de Jong 1996), and to air temperature (Richards 1989; Catto, Racey & Stephenson 1995; Walsh, Harris & Hutson 1995), as found in this study (Table 4.3). In a study by Negraeff & Brigham (1995), bat activity was related to ambient temperature, but not to other environmental parameters (wind speed, cloud cover, percentage moon face illuminated).

Wind speed affects the distribution of nocturnal insects (Peng, Fletcher & Sutton 1992), and wind-breaks and hedgerows affect insect distribution, probably because of their effect on local wind speed (Lewis 1969). In the present study, wind speed was not found to influence levels of bat activity. However, wind speed was estimated, perhaps inaccurately, on the Beaufort scale, and only one estimate was made per night. Small local changes in wind speed due to levels of shelter were not quantified, except in terms of sheltered and exposed subdivisions of main transects.

Moon phase and cloud cover both contribute to light levels during the night, which may affect the predator avoidance behaviour and feeding activity of bats. Although some neotropical frugivorous bats are found to be less active than usual or to return to day roosts when the moon is full, regardless of cloud cover (Morrison 1980), and African insectivorous bats change their activity patterns and flight behaviour in bright moonlight (Fenton *et al.* 1977), there is no evidence for lunar phobia in temperate zone insectivorous bats (Negraeff & Brigham 1995). Insect flight is, however, affected by moonlight; in some nocturnal species activity is depressed by moonlight, while other crepuscular species are active throughout moonlit nights (Bidlingmayer 1964).

No effect of season on bat activity was found in this study (Table 4.3) or by Walsh, Harris & Hutson (1995). This is somewhat surprising, as more bats may be expected to be active postlactation, after the young are weaned (Hill & Smith 1984). The pattern of activity of female bats changes with season, as they often return to the roost in the night during lactation to suckle their young (e.g. Catto, Racey & Stephenson 1995). Perhaps activity patterns remain unchanged in the early part of the night, when this study was carried out.

Land use type had a highly significant effect in the ANCOVA on total bat passes; site also had a significant effect (Table 4.3). Differences in activity levels between sites may be due either to differences in their proximity to roost sites (Kunz 1982), or to actual differences in the habitat quality between sites. Levels of bat activity were very high over rivers and lakes (Figure 4.1). Inland waters often support high levels of bat activity (e.g. Fenton 1982; Rydell *et al.* 1994; Walsh, Harris & Hutson 1995), perhaps because insect density is high there. In the Netherlands, more than one third of all bat detector records were from freshwater habitats (Kapteyn 1995). In a study of bats foraging in Ethiopian and neotropical rain forest and savannah, north temperate sub-desert, north temperate prairie, mixed deciduous and coniferous forest, and boreal forest, high levels of bat activity were consistently found to be associated with water (Fenton, Jacobson & Stone 1973).

Factors affecting the activity of Rhinolophus *species*

In this study, only eight passes of *Rhinolophus ferrumequinum* were recorded, seven of them in woodland or over pasture (Table 4.4). Radio-telemetry studies show that in spring most individuals of *Rhinolophus ferrumequinum* forage in ancient semi-natural woodland. In autumn, most individuals forage mainly over, or at the edge of, pasture (Jones & Morton 1992; Jones, Duvergé & Ransome 1995). The switch in habitat use is associated with a seasonal change in the diet of *Rhinolophus ferrumequinum*; in late summer and autumn, this species feeds predominantly on *Aphodius* dung beetles which are found in cattle pastures (Jones 1990).

In this study, *Rhinolophus hipposideros* was not recorded near water, but a very few passes were heard in woodland and over improved cattle pasture (Table 4.4). In seven habitats studied in Ireland, the foraging activity of *Rhinolophus hipposideros* was found to be highest beside water and in farmyards (McAney & Fairley 1988). In a study in France, vegetation on the banks of rivers and lakes was considered to be the most important element in the hunting habitat of *Rhinolophus hipposideros* (Barataud 1993).

Factors affecting the activity of Myotis *species and* Plecotus auritus

Overall, the activity of *Myotis* and *Plecotus* species was related to the site and the land use type, but not to the temperature or to the season (Table 4.5; Figure 4.2). However, the pattern of activity in the land use types did vary according to season and temperature (Table 4.5). Seasonal variation has been documented in the diet of *Myotis nattereri*

(Bauerová & Červený 1986), and changes in diet or insect availability according to season and temperature may explain the interaction effects. Changes in habitat use through the year have been recorded for many *Myotis* species (see below). For *Myotis mystacinus* and *Myotis daubentonii*, seasonal changes in habitat use are not related to insect distribution, but are attributed to predator avoidance behaviour. When nightly light levels are high, these species hunt in woodlands; when light intensity decreases they move into open habitats (Nyholm 1965).

Rivers and lakes are clearly important foraging areas for *Myotis* and *Plecotus* species (Figure 4.2). Unimproved grassland, improved cattle pasture, ancient semi-natural woodland and mixed plantations are also good foraging habitats for these species. In North America, *Myotis* species have been observed foraging over water and in woodland (Fenton & Bell 1979).

Myotis brandtii, recorded in this study mainly over rivers and lakes and in mixed plantations (Table 4.4), is found in locations surrounded by woodland and near lakes in Westfalen, Germany, and is considered to be a woodland species with precise habitat needs (Taake 1984). In central Europe, *Myotis brandtii* roosts are found near lowland waters (Roer 1975). *Myotis brandtii* is found in conifer plantations in Sweden, and counts of bats in suitable habitat patches are negatively affected by patch isolation (Ekman & de Jong 1996). The species avoids open spaces (de Jong 1995).

Myotis mystacinus, recorded in this study mainly over rivers and lakes and to a lesser extent in ancient semi-natural woodlands and mixed plantations, is found in Westfalen further away from woodland, and nearer to rivers, fields and parks, than *Myotis brandtii*. In spite of a preference for open habitats, *Myotis mystacinus* is considered to be more flexible in its habitat requirements than *Myotis brandtii* (Taake 1984). In Finland, female *Myotis mystacinus* feed in mixed forests in spring and early summer, and move into more open habitats, including freshwater habitats, later in the year. When hunting in forests, individual bats forage in the same areas each night and sometimes from year to year, but in the open, bats forage together (Nyholm 1965). In the Netherlands, *Myotis mystacinus* is found primarily in woodlands and shows no preference for rivers and lakes (Kapteyn 1995). *Myotis mystacinus* roosts in central Europe are found in dense woodland in mountainous areas (Roer 1975).

Myotis nattereri was found most commonly over rivers, lakes, and in ancient semi-natural woodland and mixed plantations (Table 4.4). This species feeds largely by gleaning Diptera from the surfaces of leaves (Bauerová & Červený 1986; see Chapter 2). Individuals in France foraged in deciduous woodland, in undergrowth and inside hedges.

Single trees were only visited when they were near to cover (Barataud 1993). In Sweden, *Myotis nattereri* hunts in coniferous forest or in deciduous swamp forest, often over rivers (de Jong 1995).

Myotis daubentonii feeds by trawling insects from the surfaces of rivers and lakes (Jones & Rayner 1988). In this study, *Myotis daubentonii* was most common over rivers and lakes, but was also recorded in woodland and over grassland (Table 4.4). In Scotland, this species feeds over rivers, pools and drainage ditches, and around riparian vegetation (Swift & Racey 1983; Rydell *et al.* 1994). Female *Myotis daubentonii* in Finland hunt in mixed forests early in the year, and move into open habitats or to water later on in the summer and autumn (Nyholm 1965). In the Netherlands, *Myotis daubentonii* hunts over small ponds, brooks and ditches, especially near woodlands (Kapteyn 1993), and over 80% of records of foraging *Myotis daubentonii* were over water (Kapteyn 1995). In this study, 88% of passes attributed to *Myotis daubentonii* were recorded over rivers and lakes.

In this study, *Plecotus auritus* was probably under-represented because of the low intensity of its echolocation calls (Waters & Jones 1995). An estimated 7.6% of the total bat population in Great Britain is *Plecotus auritus* (Harris *et al.* 1995), but only 0.3% of bat passes recorded for this study were attributed to this species (Table 4.2). Passes classified as *Plecotus auritus* were recorded in woodlands, and over rivers, lakes and grassland (Table 4.4). In Sweden, *Plecotus auritus* roosts are generally surrounded by deciduous woodland (Frylestam 1970), but foraging bats are found in coniferous woodland (Ekman & de Jong 1996). Radio-telemetry in Germany shows that this species forages almost exclusively in woodland (Furhmann & Seitz 1992). In Scotland, individuals of *Plecotus auritus* forage singly in woodland, remaining close to the roost and flying into the foliage to hunt (Swift & Racey 1983). In the Netherlands, 70% of bat detector *Plecotus auritus* records are from woodland (Kapteyn 1995). Populations of *Plecotus auritus* may be negatively affected by the isolation of suitable habitats (Ekman & de Jong 1996).

Factors affecting the activity of Pipistrellus *species*

In this study, passes attributed to *Pipistrellus nathusii* were heard over rivers and at Chew Valley Lake, during lactation and postlactation (Table 4.4). Although classed as a migrant winter visitor (Speakman *et al.* 1991), *Pipistrellus nathusii* has also been recorded near to this lake in spring and autumn (Barlow & Jones 1996). Thus, *Pipistrellus nathusii* appears to be present throughout the year in England, though perhaps only in small numbers. *Pipistrellus nathusii* hunts in wet deciduous forests in Germany (Jüdes 1987b) and feeds mainly on aquatic insects (Beck 1994-1995; see Chapter 2). In the Netherlands, this

species mostly hunts over water, but is also seen in woodlands and along lines of trees in agricultural areas (Kapteyn 1993; 1995).

In Scotland, *Pipistrellus pipistrellus* hunts over water, in parks, in woodland and over farmed land (Racey & Swift 1985; Rydell *et al.* 1994). In the Netherlands, *Pipistrellus pipistrellus* is found in many habitats; near water, in villages, in agricultural areas, in woodlands and near vegetation. The species is not often observed hunting over open fields (Kapteyn 1993; 1995). In Switzerland, rivers with trees, and to a lesser extent urban areas, hedges and lines of trees are important hunting habitats for *Pipistrellus pipistrellus* (Moeschler & Blant 1990). In Sweden, *Pipistrellus pipistrellus* is dependent on deciduous woodland near lakes for foraging (de Jong & Ahlén 1991), but open habitats are also used (de Jong 1995). Foraging habitat loss due to drainage and water pollution is considered to be the cause of a decline in a Swedish population of *Pipistrellus pipistrellus* which fed mostly in freshwater habitats (Gerell & Lundberg 1993).

In this study *Pipistrellus pipistrellus* was recorded approximately in accordance with its estimated relative abundance in Great Britain (Table 4.2). 45 kHz and 55 kHz *Pipistrellus pipistrellus* could be distinguished and are considered separately in terms of habitat use.

Bats classified as 45 kHz *Pipistrellus pipistrellus* were active and feeding in a wide range of land use types, particularly over rivers and lakes and in woodland (Figure 4.3) The activity, but not the feeding rate, of 45 kHz *Pipistrellus pipistrellus* was affected by temperature (Table 4.6). The activity of bats classified as 55 kHz *Pipistrellus pipistrellus* was higher over rivers and lakes than in any other land use types (Figure 4.4a), and was not affected by temperature (Table 4.7). The feeding rate of 55 kHz *Pipistrellus pipistrellus* was high over rivers and lakes, indicating that bats foraging in these habitats were catching more insects per unit of flight activity than those hunting in other habitats (Figure 4.4b). Thus, the sibling *Pipistrellus* species appear to have quite different habitat requirements. The effects of changes in river water quality on the foraging activity of the sibling species differ. Both 45 kHz and 55 kHz *Pipistrellus pipistrellus* are less active over stretches of river polluted by sewage outputs than over cleaner stretches of river, but the feeding activity in particular of 45 kHz *Pipistrellus pipistrellus* is reduced over polluted stretches (Chapter 5). Perhaps 55 kHz *Pipistrellus pipistrellus* is particularly reliant on aquatic insects, some of which (Chironomidae) are tolerant of pollution (Williams & Feltmate 1992). It seems feasible that the flight of the insects taken by 45 kHz *Pipistrellus pipistrellus* is more dependent on the air temperature than is the emergence of the aquatic insects taken by 55 kHz *Pipistrellus pipistrellus.* Emergence of aquatic insects follows a

diurnal rhythm linked to light levels, and is not correlated with water temperature (Morgan & Waddell 1961), and the abundance of nocturnal insects as measured by light trap catches is related to the air temperature (Williams 1961).

Factors affecting the activity of Nyctalus *species and* Eptesicus serotinus

The activity of bats classified as *Nyctalus leisleri*, affected only by land use type (Table 4.8), was highest over rivers, lakes, and over improved cattle pasture, although all land use types were used (Figure 4.5). Very little has been published on the foraging habitat use of this species, though a roost was found in Ireland among small fields with hedges, mature trees, a stream and a canal nearby (Sullivan *et al.* 1993).

In a survey of habitat use by *Nyctalus noctula* in a nature reserve in Poland, activity was found to be highest over rivers, along forest and meadow borders, and in very small villages. Very little activity was recorded in deciduous and coniferous forests (Rachwald 1992). In the Netherlands, *Nyctalus noctula* was often found hunting over rivers and canals (Kapteyn 1993), and in open parts of woodlands in early evening (Kapteyn 1995). In the Czech Republic, this species hunts over ponds in woodlands and in fields, in parks, at the outskirts of towns, in woodland clearings, and over roads, old lanes and fields (Gaisler, Hanák & Dungel 1979). In Germany, radio telemetry revealed that individuals of *Nyctalus noctula* foraged mainly over a lake in the early evening, and in an urban area near street lamps and a wood later in the night (Kronwitter 1988). In this study, the activity of bats classified as *Nyctalus noctula* was also high near lakes and over improved cattle pasture, and low in woodlands, but villages did not support high levels of activity (Figure 4.6).

Echolocation calls of *Nyctalus* species are of relatively high intensity (Ahlén 1990), which may explain why these species are over-represented in bat detector studies such as this (Table 4.2).

Passes attributed to *Eptesicus serotinus* were recorded mostly over rivers and lakes and in grassland and other open habitats, especially in improved cattle pastures where *Aphodius* dung beetles, the preferred food of this species (Catto, Hutson & Racey 1994; see Chapter 2), are expected to be plentiful. Only one pass was heard in woodland (Table 4.4). This species forages in the crowns of mature trees in Germany, and is not especially attracted to water (Hildenhagen & Taake 1982). In the Netherlands, *Eptesicus serotinus* avoids woodland and forages over canals, in open habitats and cultivated areas (Kapteyn

1993; 1995). Radio-telemetry studies in England show that *Eptesicus serotinus* feeds mainly over cattle pastures and near white street lamps (Catto *et al.* 1996).

Woodland edges

In this study, bats were not found to be selecting woodland edges for foraging, although other studies show that bats are very active along woodland edges (Rachwald 1992; Walsh, Harris & Hutson 1995). It is possible that bats do not prefer woodland edges over woodland interior, but that studies which rely partly on visual observation of bats are biased towards edges. Flying bats may be more obvious along woodland edges than in darker woodland interiors. Alternatively, bats do prefer woodland edges, but the small sample size of this study (nine woodlands, each sampled three times) made it impossible to detect the preference.

Main transect subdivisions

Bats probably selected sheltered subdivisions of transects for foraging because of increased insect densities there. Flying insects accumulate in sheltered areas (Lewis 1969) and the distribution of nocturnal insects especially is influenced by wind speed (Peng, Fletcher & Sutton 1992). Bats flying near wind-breaks in open fields in the Czech Republic were thought to be feeding on the concentrations of insects there rather than using them for navigation (Gaisler & Kolibáč 1992; see Limpens & Kapteyn 1991 and Chapter 1).

Bats did not select woodland rides in this study, although other studies have documented a preference for open areas and rides in woodland. Walsh & Mayle (1991) found bat activity to be higher along woodland rides than in other woodland habitats except over ponds in woodland. In a study in the Czech Republic, bat activity was very high in woodland glades (Gaisler & Kolibáč 1992).

Many studies document bats hunting concentrations of insects around street lamps (e.g. Fenton 1982; Furlonger, Dewar & Fenton 1987; Kronwitter 1988; Rydell 1992; Blake *et al.* 1994). In this study, only three villages were visited and no selection for lit areas was recorded.

Social / song-flight calls

Social calls are produced by *Pipistrellus pipistrellus* throughout the year in agonistic interactions; the male song-flight display is carried out only in autumn. During song-flight males remain in small territories and produce calls on average 1.7 times per second

(Lundberg & Gerell 1986). An increase in the number of social / song-flight calls recorded would therefore be expected to occur in autumn. However, there was no obvious seasonal variation in the levels of these calls. There is no clear reason why 45 kHz *Pipistrellus pipistrellus* should produce social / song-flight calls less frequently than 55 kHz *Pipistrellus pipistrellus*, as found in this study.

Conclusions

The study described in this chapter shows that, in spite of differences in echolocation call structure and intensity (Waters & Jones 1995), broad-band acoustic methods can be used to identify the foraging habitats used by different bat species. Although the multivariate analysis of call parameters does not allow the identification of bat species from calls with complete certainty, it is objective and repeatable, unlike many other methods which rely on the skill of the observer and the use of tuned detectors (Kapteyn 1993; 1995).

Above all, this study shows that bats make disproportionate use of rivers and lakes for hunting. About 3% of the surface area of the British Isles is covered by fresh water (Bunce & Heal 1984), but most of the foraging bats are found there. We need to know which types of rivers, lakes, and ponds are preferred by bats, and how freshwater habitats can be managed to attract more foraging bats. Many factors affect the invertebrate communities found in and around rivers and lakes, such as flow rate, substrate, eutrophication, acidification, pollution, neighbouring land use and water abstraction (Jeffries & Mills 1990). There is some evidence to suggest that rivers in city parks support fewer bats and less diverse bat communities than nearby rural lakes (Kurta & Teramino 1992), and that rivers without vegetation on their banks may be less attractive to bats than rivers with trees (Racey & Swift 1985; Rydell *et al.* 1994). Urban streams support insect communities of a different composition than do rural streams (Jones & Clark 1987), and vegetation on river banks and in the water affects the river insect community (Jeffries & Mills 1990). All these factors warrant further study from the perspective of bat conservation. Also, possible effects of changes in water quality on insects and bats need to be investigated. Changes in water quality affect aquatic invertebrate communities (Williams & Feltmate 1992), and are likely to affect different bat species in different ways (Chapter 5).

Other habitats, such as cattle pasture and woodland, are important foraging habitats for some species of bat, and should also be managed to conserve or benefit insect populations. In pasture, hedgerows, and in woodlands, rides and dead wood, provide good habitats for insect growth and reproduction (Fry & Lonsdale 1991). Emergent hedgerow

trees are important in the life-cycles of many Diptera, and may benefit bats (Peng, Sutton & Fletcher 1992).

Land use change, leading to changes in populations of bats, may occur directly due to the activities of man, or as a consequence of global climatic change (Scheel, Vincent & Cameron 1996). Not only the area of habitats available, but also their configuration is likely to affect the animal populations that feed or roost in them. In one study, bats used habitat corridors as hunting habitats, and *Myotis brandtii*, *Myotis nattereri* and *Plecotus auritus* avoided all open habitats, while *Pipistrellus pipistrellus* did not (de Jong 1995). Habitat connectivity is likely to be important in facilitating the movements of bats between suitable habitats and roosts (Walsh 1995). In theory, habitat fragmentation is likely to lead to a decline in bat populations, especially in those of *Rhinolophus* and *Myotis* species (Bright 1993). More work needs to be done to test the validity of such theories for individual species of bat. The habitat needs of bat species differ, and their individual requirements should be taken into account in future habitat management schemes.

Table 4.1 Land use types, main transect subdivisions, and replicate sites in each land use type. The Ordnance Survey grid references are of the approximate centre of the site.

Land use type (abbreviation)	Subdivisions	Replicate sites	OS grid reference
1. Rivers (Ri)	sheltered/exposed	Congresbury Yeo	ST 44 63
		River Avon	ST 67 68
		River Chew	ST 65 65
2. Lakes (La)	sheltered/exposed	Upper and Lower Reservoir	ST 59 55
		Chew Valley Lake	ST 57 61
		Blagdon Lake	ST 51 60
3. Unimproved grassland (Ug)	sheltered/exposed	Weston Moor	ST 43 73
		Folly Farm	ST 60 60
		Fields near Littlewood Pool	ST 45 66
4. Amenity grassland (Ag)	sheltered/exposed	Bristol and Clifton Golf Club	ST 52 72
		Mendip Springs Golf Club	ST 43 61
		Lansdown Golf Club	ST 71 69
5. Improved cattle pasture (Ip)	sheltered/exposed	Reservoir Farm	ST 52 67
		Fields near Brockley Hall	ST 46 67
		Fields near Wrington	ST 48 62
6. Arable land (Al)	sheltered/exposed	Fields off Norton Lane	ST 59 64
		Fields near Chew Magna	ST 58 62
		Fields near Keynsham	ST 66 67
7. Villages (Vi)	lit/unlit	Long Ashton	ST 54 70
		Yatton	ST 43 65
		Backwell	ST 48 68
8. Ancient semi-natural woodland (Aw) (& edge transect)	on path/off path	Bourton Combe	ST 50 68
		Cheddar Wood	ST 44 55
		West Wood and Weston Big Wood	ST 45 75
9. Conifer plantations (Cp) (& edge transect)	on path/off path	Wrington Warren	ST 48 65
		Stockhill	ST 55 50
		Rowberrow Warren	ST 46 58
10. Mixed plantations (Mp)(& edge transect)	on path/off path	Ashton Hill Plantation	ST 52 70
		Lord's Wood	ST 63 62
		Gare Hill	ST 78 40

Table 4.2 Numbers of bat passes on all 90 main transects attributed to each bat species. 83% of bat passes (including all *Pipistrellus* species passes) were identified to species level; the remaining 17% could be assigned to a species group (*Myotis* and *Plecotus* species or *Nyctalus* species and *Eptesicus serotinus*). The percentages of the total number of bat passes attributed to each species are compared to British population estimates (Harris *et al.* 1995). An asterisk indicates those species or groups for which statistical analysis was carried out. Habitat preferences of other species are shown in Table 4.4.

Species	**No. of bat passes counted**	**% of total**	**% of total bat population**
Rhinolophus ferrumequinum	8	0.1	0.2
Rhinolophus hipposideros	13	0.2	0.5
Myotis brandtii	112	2.0	1.1
Myotis mystacinus	33	0.6	1.5
Myotis nattereri	31	0.6	3.8
Myotis daubentonii	276	5.0	5.7
Plecotus auritus	17	0.3	7.6
Pipistrellus nathusii	14	0.3	?
45 kHz *Pipistrellus pipistrellus* *	1654	30	76
55 kHz *Pipistrellus pipistrellus* *	1873	34	(*P. pipistrellus*)
Nyctalus leisleri *	140	2.5	0.4
Nyctalus noctula *	360	6.5	1.9
Eptesicus serotinus	37	0.7	0.6
Subtotal *Myotis* and *Plecotus* species (including 427 unidentified passes) *	896	16	19.7
Subtotal *Nyctalus* species and *Eptesicus serotinus* (including 524 unidentified passes)	1061	19	2.9
Total *	**5519**	**100**	**99.3**

Table 4.3 An ANCOVA for effects of site, land use type and season on log transformed bat passes (all species) with temperature as a covariate shows that land use has a highly significant effect on bat activity. There is also a significant temperature effect and significant differences in numbers of bat passes between sites. See Figure 4.1. In all tables, df = degrees of freedom, Adj.MS = adjusted mean squares, n.s. = not significant.

Source of variation	**df**	**Adj.MS**	**F**	***P***
site (nested in land use type)	20	1.75	2.17	<0.05
land use type	9	11.7	14.6	<0.0001
season	2	0.837	1.04	n.s.
temperature (covariate)	1	5.97	7.44	<0.01
error	57	0.80		
total	89			

Table 4.4 Numbers of bat passes attributed to the nine species of bat which were recorded least frequently, or the counts of which failed to conform to the assumptions of ANCOVA, shown in relation to the ten land use types. **Ri** = rivers, **La** = lakes, **Ug** = unimproved grassland, **Ag** = amenity grassland, **Ip** = improved pasture, **Al** = arable land, **Vi** = villages, **Aw** = ancient semi-natural woodland, **Cp** = conifer plantations, **Mp** = mixed plantations.

Species	Total no. of passes	Ri	La	Ug	Ag	Ip	Al	Vi	Aw	Cp	Mp
R. ferrumequinum	8	0	0	2	0	2	0	1	2	1	0
R. hipposideros	13	0	0	0	0	2	0	0	5	4	2
M. brandtii	112	23	42	7	3	6	1	0	6	1	23
M. mystacinus	33	9	8	3	1	1	1	0	2	1	7
M. nattereri	31	10	8	2	0	2	1	0	3	0	5
M. daubentonii	276	126	117	4	0	8	2	0	10	1	8
P. auritus	17	2	2	1	2	1	0	0	3	2	4
P. nathusii	14	3	11	0	0	0	0	0	0	0	0
E. serotinus	37	6	13	2	3	7	4	1	1	0	0

Table 4.5 An ANCOVA for effects of site, land use type and season on log transformed counts of *Myotis* and *Plecotus* species passes, with temperature as a covariate. The activity of these species is significantly influenced by site, land use type, and by the interaction terms. This means that the effect of land use type is not equal in all seasons and at all temperatures. See Figure 4.2.

Source of variation	**df**	**Adj.MS**	**F**	***P***
site (nested in land use type)	20	1.24	4.61	<0.0001
land use type	9	1.68	6.23	<0.0001
season	2	0.472	1.75	n.s.
temperature (covariate)	1	0.095	0.35	n.s.
land use type * season interaction	18	0.810	2.20	<0.01
land use type * temperature interaction	9	0.807	2.99	<0.05
error	30	0.270		
total	89			

Table 4.6 ANCOVAs for effects of site, land use type and season on log transformed counts of 45 kHz *Pipistrellus pipistrellus* passes, and on square roots of logged buzz ratios, with temperature as a covariate. Land use type has a highly significant effect on the activity of this species; there is also a significant temperature effect. The buzz ratio is not affected by any of the measured variables. See Figure 4.3.

Source of variation - Passes	**df**	**Adj.MS**	**F**	***P***
site (nested in land use type)	20	1.68	1.72	n.s.
land use type	9	7.76	7.95	<0.0001
season	2	0.664	0.68	n.s.
temperature (covariate)	1	6.55	6.71	<0.05
error	57	0.976		
total	89			

Source of variation - Buzz ratios	**df**	**Adj.MS**	**F**	***P***
site (nested in land use type)	20	0.024	0.86	n.s.
land use type	9	0.026	0.94	n.s.
season	2	0.042	1.53	n.s.
temperature (covariate)	1	0.064	2.32	n.s.
error	57			
total	89			

Table 4.7 ANCOVAs for effects of site, land use type and season on log transformed counts of 55 kHz *Pipistrellus pipistrellus* passes, and on square roots of logged buzz ratios, with temperature as a covariate. Land use type is the only measured factor significantly influencing the activity of this species. Both land use and site significantly influence the buzz ratios. See Figure 4.4.

Source of variation - Passes	**df**	**Adj.MS**	**F**	***P***
site (nested in land use type)	20	2.03	1.60	n.s.
land use type	9	14.3	11.3	<0.0001
season	2	1.76	1.39	n.s.
temperature (covariate)	1	3.21	2.53	n.s.
error	57	1.27		
total	89			

Source of variation - Buzz ratios	**df**	**Adj.MS**	**F**	***P***
site (nested in land use type)	20	0.038	2.37	<0.01
land use type	9	0.066	4.15	<0.0001
season	2	0.015	0.93	n.s.
temperature (covariate)	1	0.001	0.07	n.s.
error	57			
total	89			

Table 4.8 An ANCOVA for effects of site, land use type and season on square roots of log transformed counts of passes attributed to *Nyctalus leisleri* with temperature as a covariate shows that land use type is the only measured factor with a significant influence on the activity of this species. See Figure 4.5.

Source of variation	**df**	**Adj.MS**	**F**	***P***
site (nested in land use type)	20	0.091	1.56	n.s.
land use type	9	0.440	7.52	<0.0001
season	2	0.138	2.36	n.s.
temperature (covariate)	1	0.009	0.15	n.s.
error	57	0.059		
total	89			

Table 4.9 An ANCOVA for effects of site, land use type and season on square roots of log transformed counts of passes attributed to *Nyctalus noctula* with temperature as a covariate shows that land use type is the only factor significantly influencing the activity of this species. See Figure 4.6.

Source of variation	**df**	**Adj.MS**	**F**	***P***
site (nested in land use type)	20	0.107	1.23	n.s.
land use type	9	0.800	9.15	<0.0001
season	2	0.181	2.06	n.s.
temperature (covariate)	1	0.061	0.690	n.s.
error	57	0.088		
total	89			

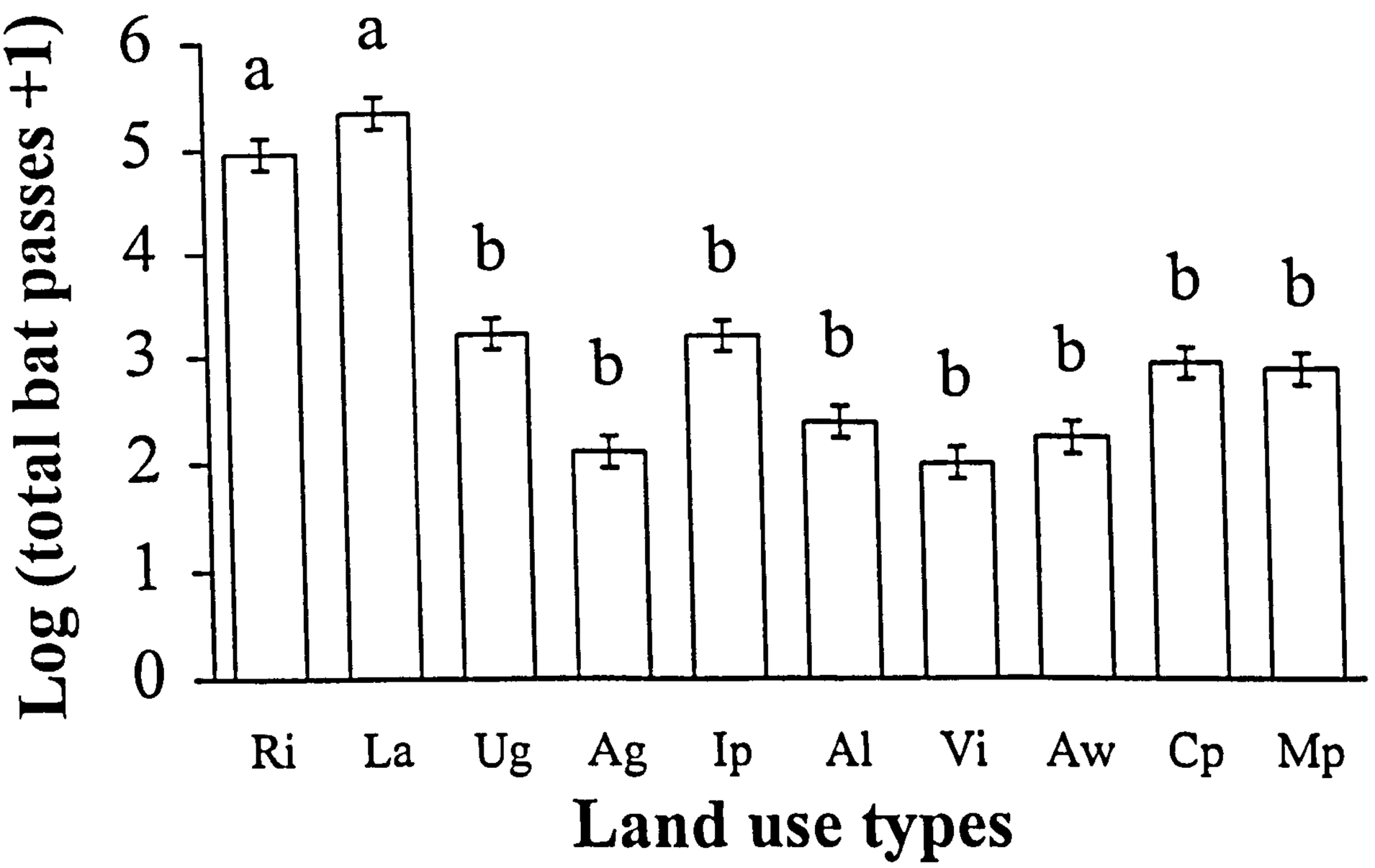


Figure 4.1 Adjusted mean log transformed counts of total bat passes recorded in each of the ten land use types (abbreviations as in Table 4.1). Groups of land use types supporting levels of activity which are not significantly different from one another are indicated by the same letter. In all figures, the bars represent the adjusted mean of nine main transects (three sites visited three times each), and the standard deviations are shown.

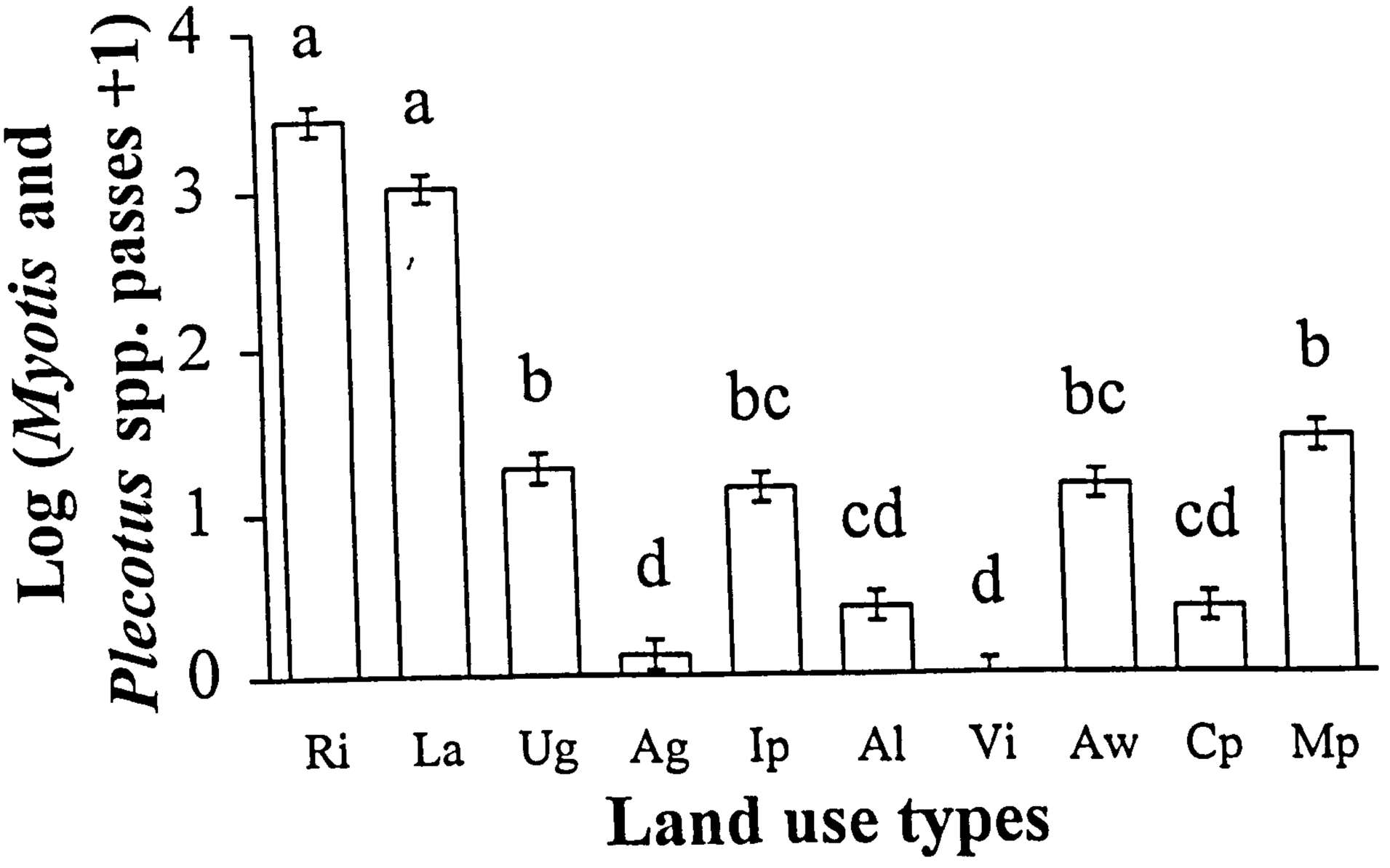
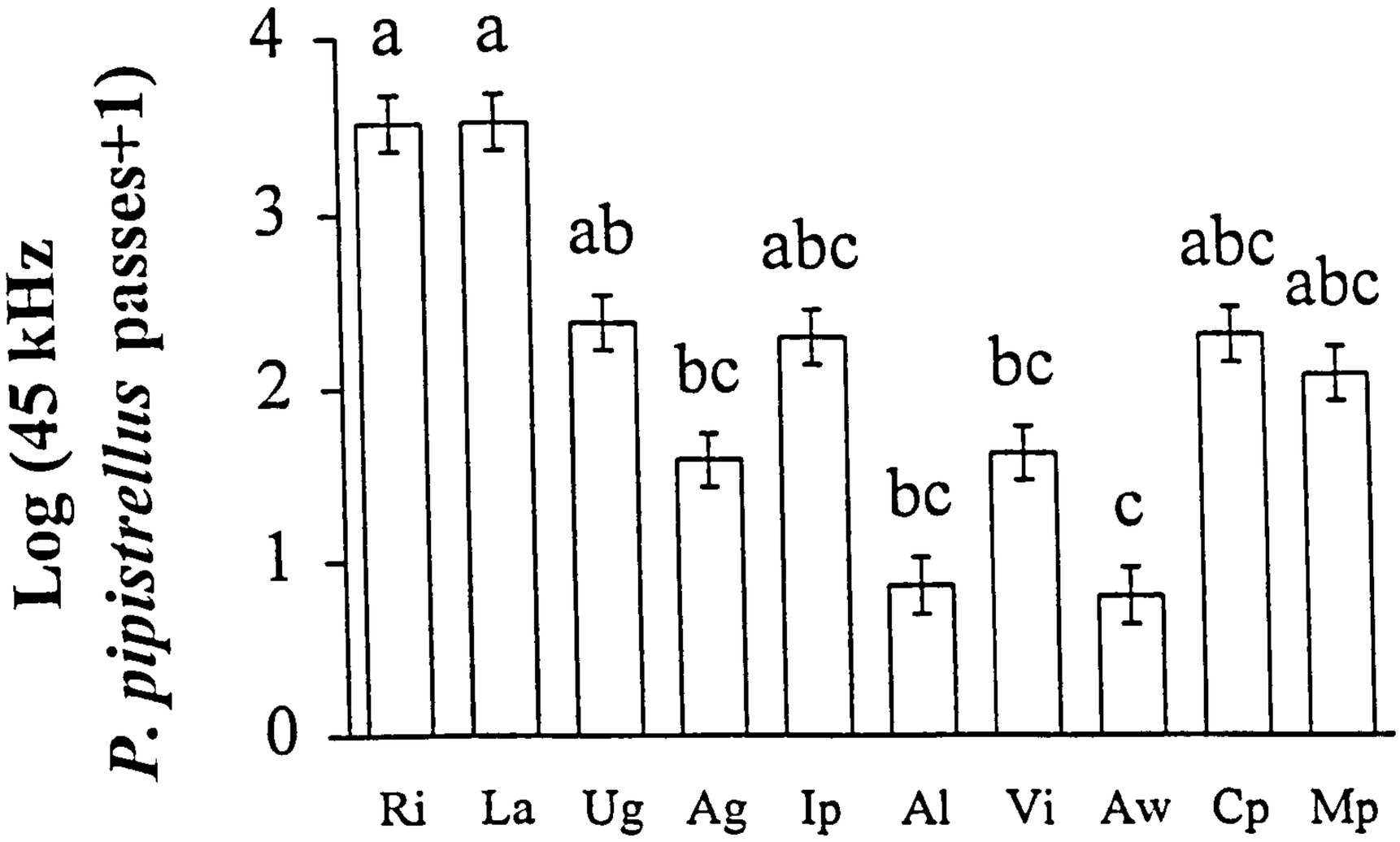


Figure 4.2 Adjusted mean log transformed counts of *Myotis* and *Plecotus* species passes recorded in each of the ten land use types (abbreviations as in Table 4.1). Groups of land use types supporting levels of activity which are not significantly different from one another are indicated by the same letter.

(a)



(b)

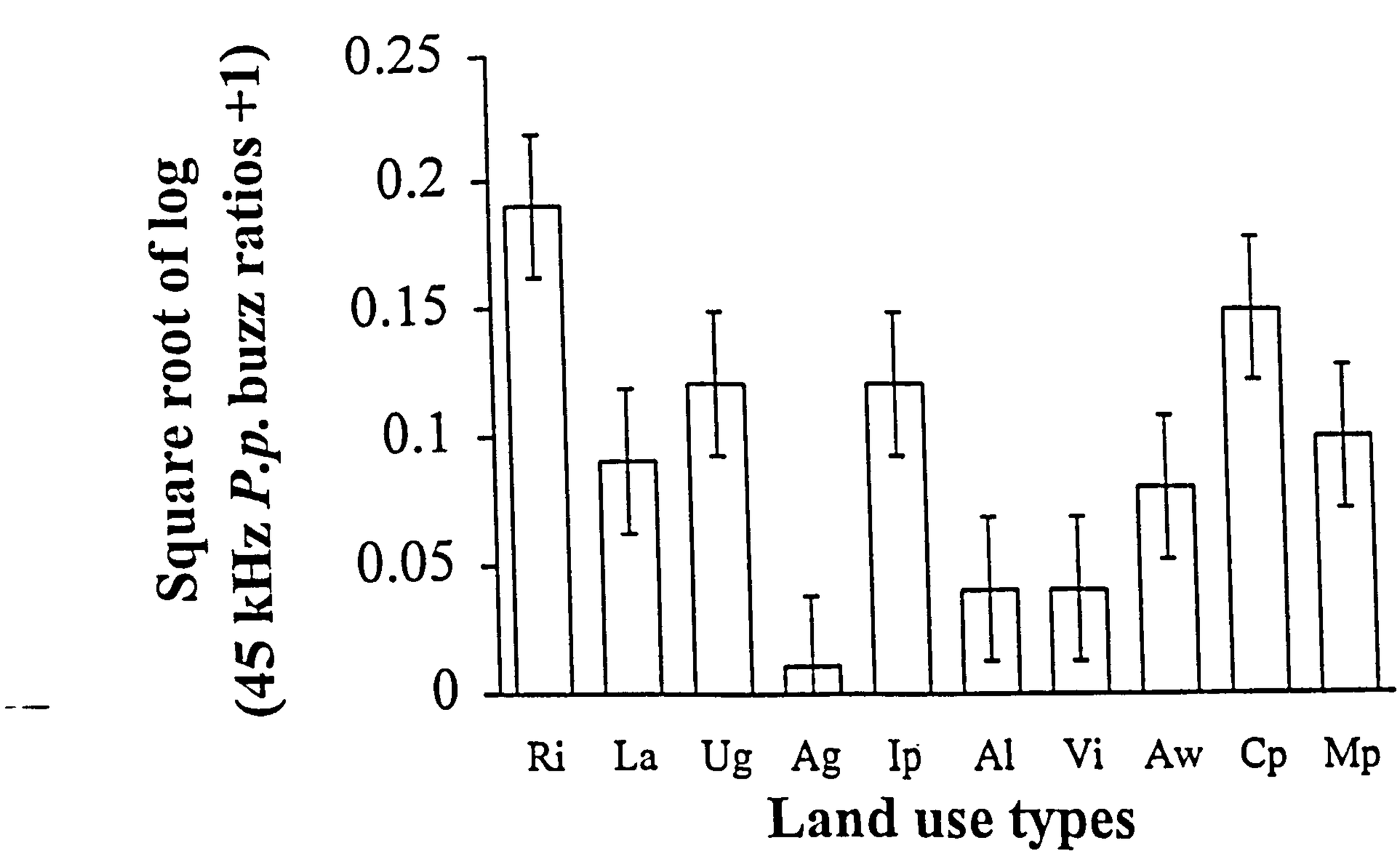
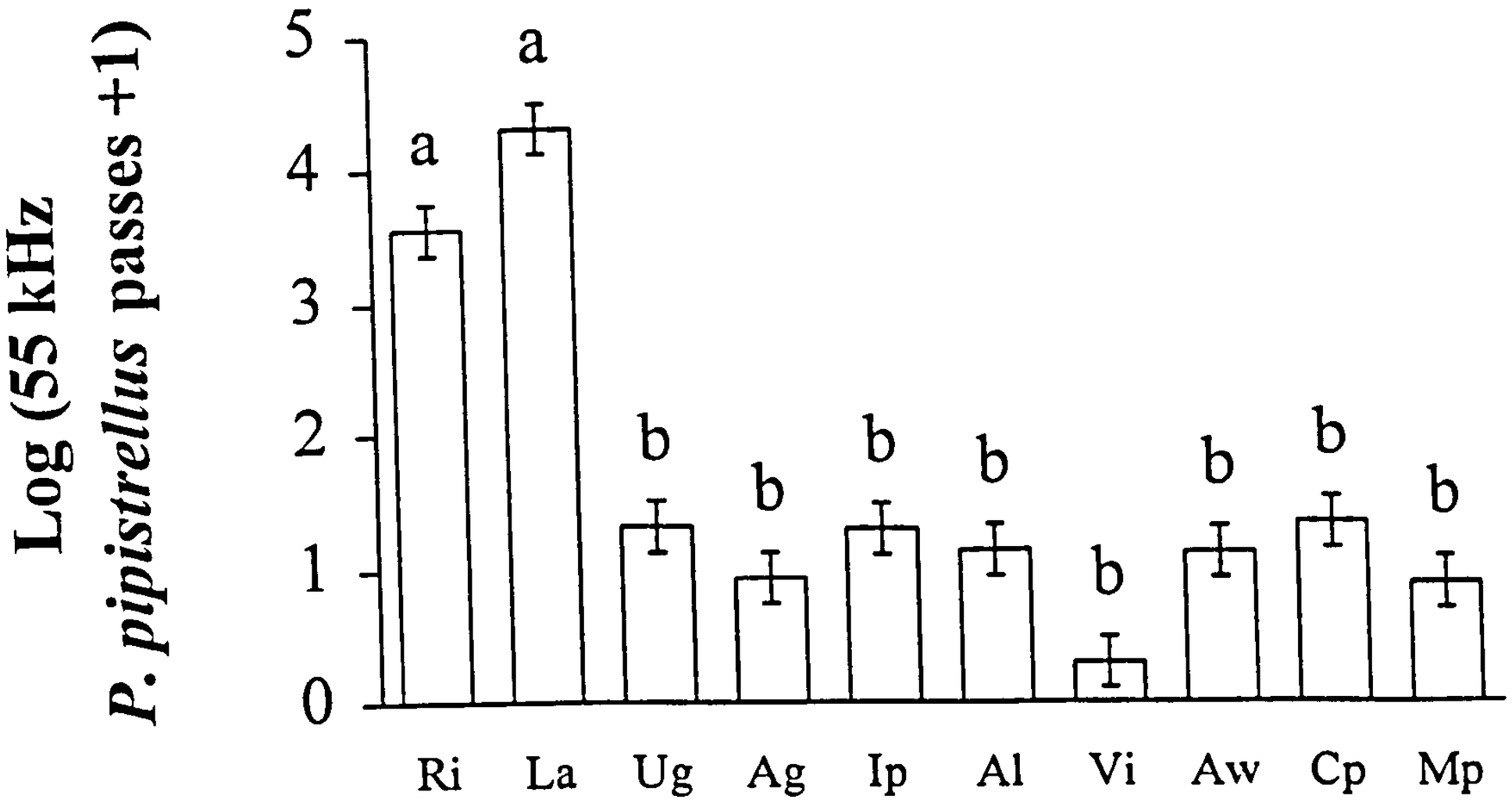


Figure 4.3 Adjusted mean log transformed counts of passes (**a**) and square roots of logged buzz ratios (**b**) attributed to 45 kHz *Pipistrellus pipistrellus* recorded in each of the ten land use types (abbreviations as in Table 4.1). Groups of land use types supporting levels of activity which are not significantly different from one another are indicated by the same letter.

(a)



(b)

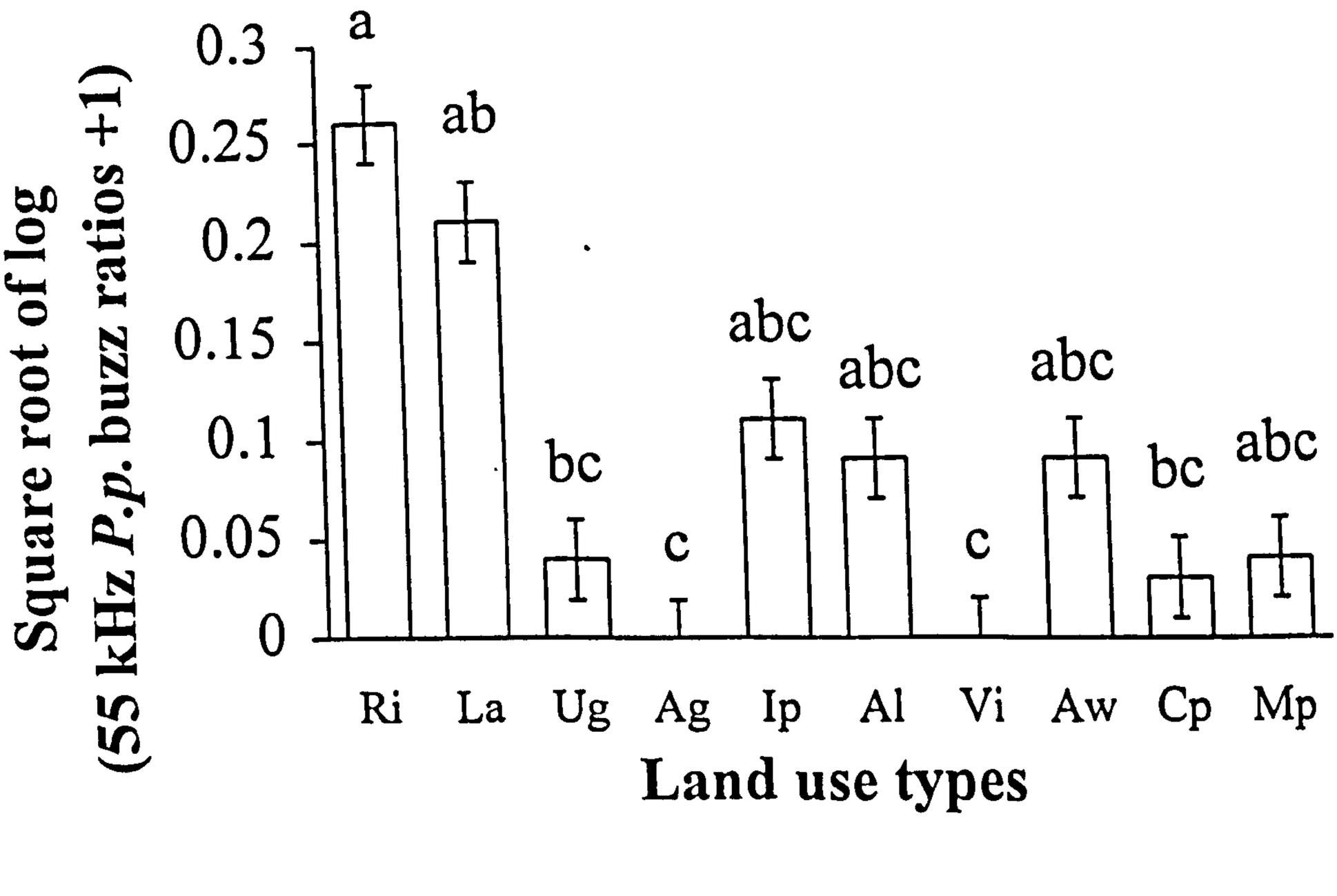


Figure 4.4 Adjusted mean log transformed counts of passes (a) and square roots of logged buzz ratios (b) attributed to 55 kHz *Pipistrellus pipistrellus* recorded in each of the ten land use types (abbreviations as in Table 4.1). Groups of land use types supporting levels of activity and buzz ratios which are not significantly different from one another are indicated by the same letter.

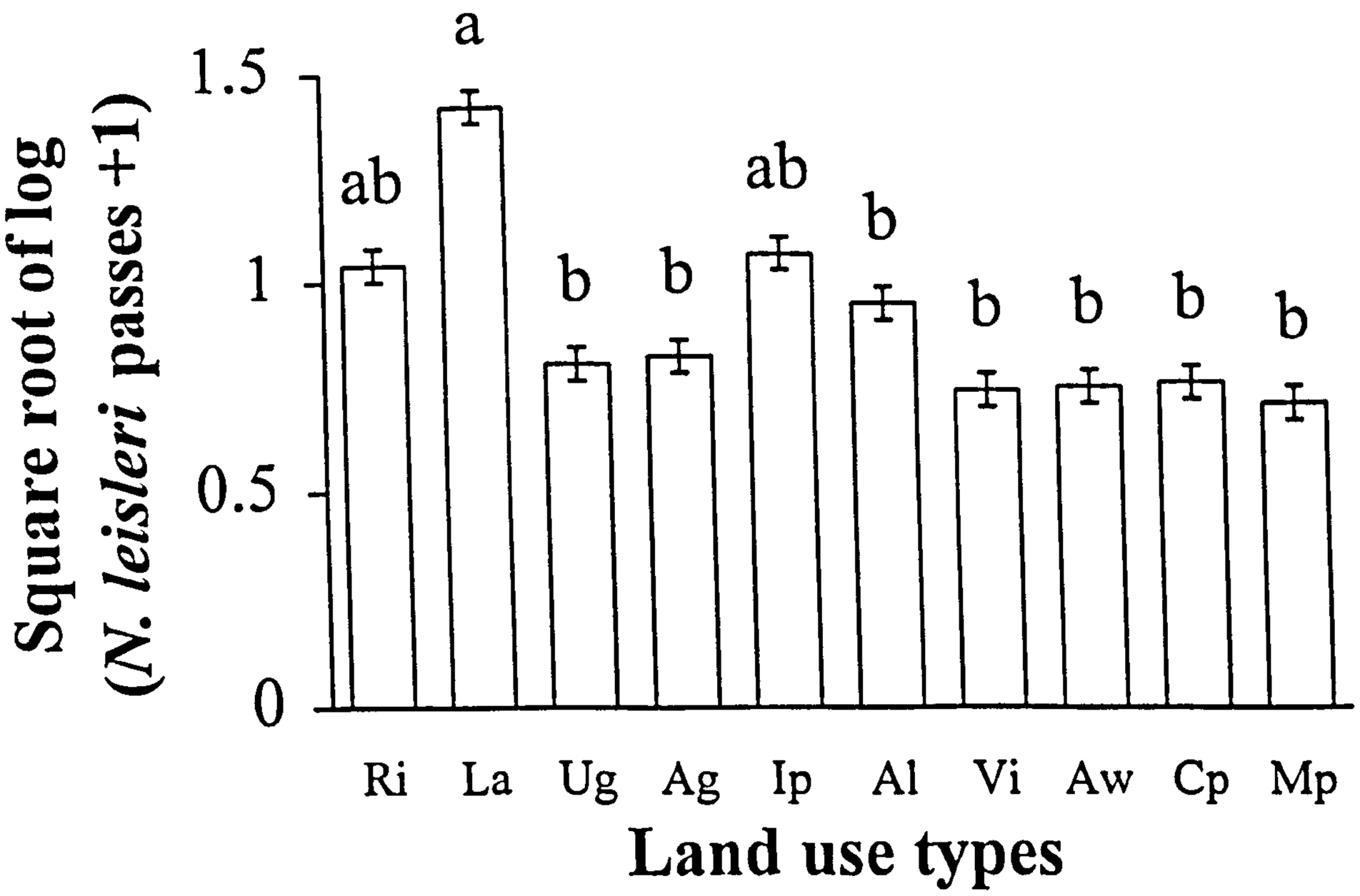


Figure 4.5 Adjusted mean square roots of log transformed counts of passes attributed to *Nyctalus leisleri* recorded in each of the ten land use types (abbreviations as in Table 4.1). Groups of land use types supporting levels of activity which are not significantly different from one another are indicated by the same letter.

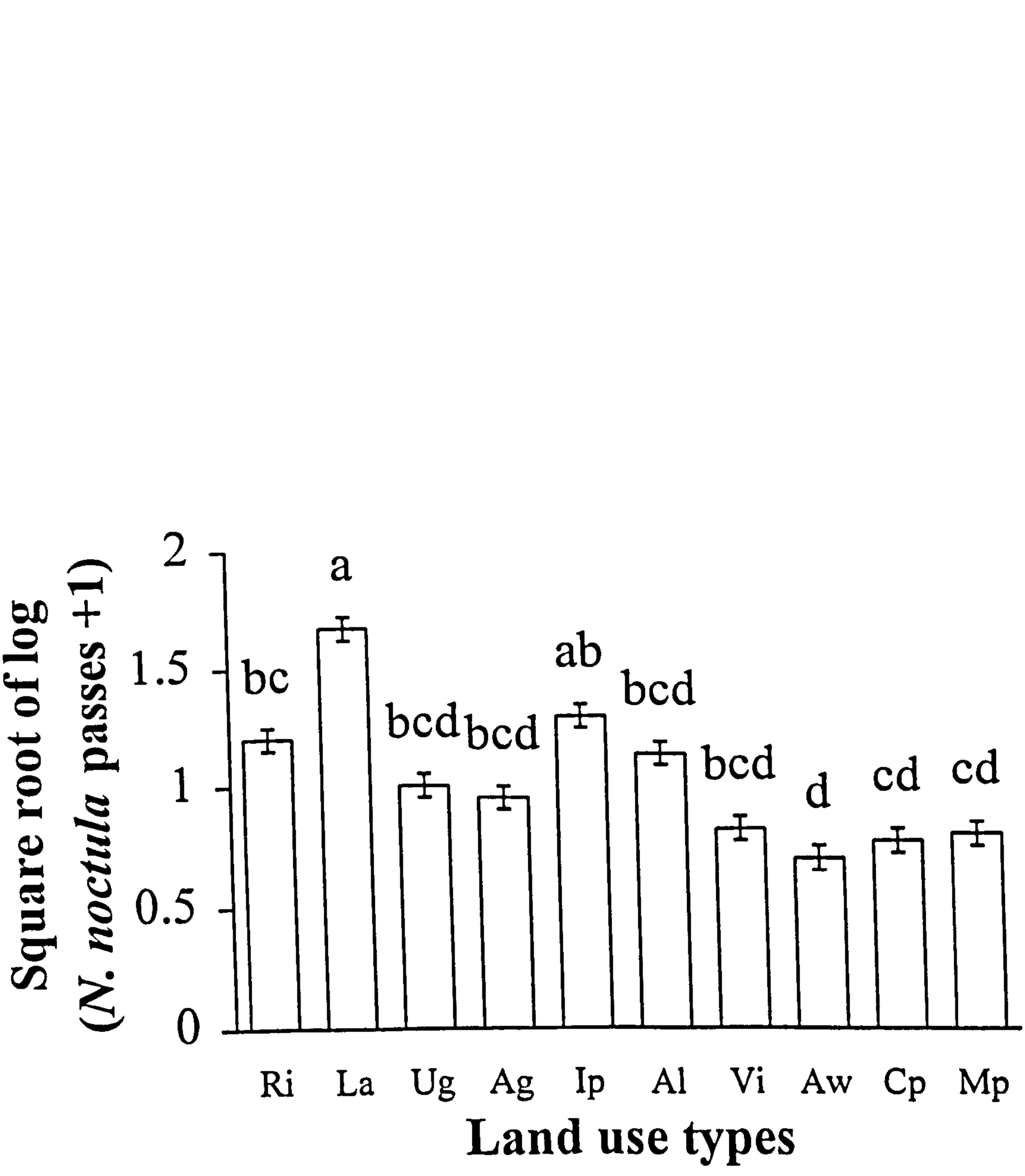


Figure 4.6 Adjusted mean square roots of log transformed counts of passes attributed to *Nyctalus noctula* recorded in each of the ten land use types (abbreviations as in Table 4.1). Groups of land use types supporting levels of activity which are not significantly different from one another are indicated by the same letter.

FIVE

Effects of sewage on the activity of bats foraging over rivers

Vaughan, N., Jones, G. & Harris, S (1996) Effects of sewage effluent on the activity of bats (Chiroptera: Vespertilionidae) foraging along rivers. *Biological Conservation*, in press, is based on this chapter.

FIVE

Effects of sewage on the activity of bats foraging over rivers

Summary

In order to investigate how a decline in river water quality might affect the foraging behaviour of bats over rivers, bat activity and feeding rates were measured at sites upstream and downstream from 19 sewage outputs. Paired sampling was used to control for variation in bat activity due to environmental parameters, and bat species groups could be identified from broad-band recordings of echolocation calls. Overall bat activity and foraging activity were reduced downstream from sewage outputs, by 11% (total reduction in passes) and 28% (total reduction in buzzes). Both 45 kHz and 55 kHz Pipistrellus pipistrellus *were less active at downstream sites than at upstream sites (total reduction in activity was 55% for 45 kHz* Pipistrellus pipistrellus *and 51% for 55 kHz* Pipistrellus pipistrellus*). Individuals of 45 kHz* Pipistrellus pipistrellus *concentrated their foraging effort at upstream sites (total reduction in counts of buzzes was 87%), while* Myotis *species foraged at higher rates downstream from outputs, than upstream (total increase in foraging rate was 112%). For the conservation of* Pipistrellus pipistrellus, *the maintenance of high standards of water quality may be important.* Myotis daubentonii *may be able to benefit from pollution.*

Introduction

The foraging activity of bats is extremely high over rivers and lakes, but the characteristics of inland waters which make them attractive to bats are unknown (Rydell *et al.* 1994; Walsh & Harris 1996; see Chapter 4). Water quality affects riparian vegetation (Holmes & Newbold 1984), and the emergent aquatic insects upon which bats feed (Williams & Feltmate 1992). While bat numbers have been decreasing in Western Europe (Chapter 1), there has been a decline in river water quality in England and Wales (Garland 1991; National Rivers Authority 1991), with a recent slight improvement (National Rivers Authority 1994). If rivers with low water quality are poor foraging habitats for bats, declines in water quality may contribute to declines in bat populations.

The decline in water quality is due primarily to agricultural practices and, to a lesser extent, to industry and urbanisation. However, pollution from agricultural runoff has a non-point source, and is found in almost all lowland rivers and streams in Britain (Malanson 1993). The effects of this agricultural pollution would be difficult to quantify. Pollution from sewage treatment works brings about a local decline in water quality. Treated sewage contains organic matter, toxins such as ammonia, and nutrient salts (phosphate and nitrate), which can result in eutrophication (Hynes 1971). Eutrophic waters are defined as having high levels of nutrients, productivity, phytoplankton, organic matter, phosphate and nitrate. Eutrophication leads to changes in the river invertebrate fauna (Jeffries & Mills 1990), and the biomass and diversity of insects emerging from rivers is reduced downstream from sewage outputs (Avery 1970; Whitehurst & Lindsey 1990).

In this study, the discharge of treated sewage into rivers was used as a model system to indicate how widespread declines in water quality might affect bat activity. If declines in river water quality have a negative effect on insect and bat populations, bat activity and bat foraging activity would be expected to be lower downstream from sewage outputs than upstream.

Methods

Sewage treatment works

Nineteen sewage treatment works, owned and managed by Wessex Water and discharging into rivers and streams in south-west England, were chosen for this study. The sewage treatment works varied greatly in terms of output and estimated width of discharge river (see Table 5.1).

The sewage treatment works were visited in daylight so that sampling could be planned. An upstream site and a downstream site were chosen near each works. Each site was linear and 25 m long. The downstream site began close to the main sewage output (usually 1 m, up to 20 m if access was difficult). The upstream site was matched to the downstream site in terms of vegetation and land use. It was approximately 200 m from the downstream site. Both sites contained two sample points, one at each end. The sample points were 25 m apart; one sample point was proximal to the sewage output, the other distal.

Sampling procedure

Bat activity and bat foraging activity upstream and downstream from each sewage treatment works were recorded on one night between 10 July 1994 and 30 September 1994. Paired sampling was used to control for variation in bat activity due to environmental parameters. Sampling started 30 minutes after sunset, and continued for 35 minutes with a five-minute break.

Upstream and downstream sites were sampled simultaneously by two people holding sound recording equipment at waist height. One person sampled each site. The order in which the two sample points within the sites were visited was randomised, so that each person recorded bats in one sample point (early) for 15 minutes, then had five minutes in which to move to the other sample point before making a second 15-minute recording (late).

Recording equipment

Each person was equipped with an S-25 bat detector set to lower bat echolocation calls to one-sixteenth of their actual frequency by frequency division. This made it possible to

record calls in real time. The bat detectors were linked to two Professional Walkmans containing metal cassettes (see Chapter 3 page 57 for details of equipment). The high frequency gain on the two bat detectors was calibrated with the aid of an ultrasound generator (Ultra Sound Advice, London; GT1), and the recording levels of the Walkmans were equal. This meant that the sensitivity to bat calls of any combination of bat detector and Walkman was similar. The combinations of equipment used at each site were randomised.

Sound analysis

The 60 minutes of recordings made each night were analysed using a Sonagraph (see page 58). Analysis was carried out blind. The number of bat passes recorded at each site was used as an indication of bat activity.

From recordings made with bat detectors set to frequency division (Chapter 3) it was clear that it would not be possible to identify all species of bat, although they could all be recorded with this broad-band method (Chapter 1). The 16 species of bat found in Great Britain can be placed in groups according to the peak frequency and duration of their echolocation calls after frequency division (Ahlén 1990). A method to distinguish these species groups was developed and tested using recordings on frequency division of bats leaving known roosts, where bats had been caught and identified in the hand (Chapter 3).

Calls made by *Myotis* species, *Plecotus* species, and probably *Barbastella barbastellus* (only one individual recorded) were similar in structure (FM) when recorded after frequency division. However, *Barbastella barbastellus* and *Myotis bechsteinii* are extremely rare in south-west England (Jones & Jayne 1988; Arnold 1993), and *Plecotus* species produce very low-intensity echolocation calls (Ahlén 1990). *Myotis nattereri* rarely feeds on aquatic insects (Chapter 2), and is uncommon in south-west England (Jones & Jayne 1988; Arnold 1993). It is assumed that these species were scarce or absent in this study. Therefore, broad-band calls of less than 5 ms duration which swept down in frequency from 90-30 kHz were assumed to have been produced mainly by *Myotis daubentonii*, *Myotis brandtii*, or *Myotis mystacinus*, here referred to as *Myotis* species. Of these, *Myotis daubentonii* is likely to be the most abundant, as it is adapted to feed over water (Jones & Rayner 1988).

Calls made by *Nyctalus noctula*, *Nyctalus leisleri* and *Eptesicus serotinus* were similar in structure after frequency division. Bats in this species group, recorded leaving roosts, produced intense calls with constant frequency components which peaked at 17-28 kHz. FM/CF calls exceeding 10 ms duration in this frequency range were assumed to have

been produced by *Nyctalus* species or *Eptesicus serotinus*. In south-west England, *Nyctalus noctula* is much more common than *Nyctalus leisleri* (Jones & Jayne 1988; Arnold 1993).

Bats producing calls with peak frequency of less than 49 kHz were classified as 45 kHz *Pipistrellus pipistrellus*, those producing calls with peak frequency of more than 52 kHz were classified as 55 kHz *Pipistrellus pipistrellus* (Jones & van Parijs 1993). A very small proportion (< 1%) of bats of this species produce echolocation calls with peak frequencies between 49 and 52 kHz. These bats were classified as unidentified *Pipistrellus pipistrellus*. All three types produced FM/CF calls with a constant frequency component of 5-7 ms duration. Most of the energy in the calls was concentrated in a narrow frequency band in this constant-frequency component. No bats were identified as *Pipistrellus nathusii*.

As well as bat passes, terminal buzzes recorded at each site were counted (Griffin, Webster & Michael 1960) and used to quantify the use of each site by bats for foraging. A count of terminal buzzes is a measure of foraging effort per unit of time in this study. Bat feeding activity was also expressed as the ratio of terminal buzzes to bat passes. This is a measure of foraging effort per unit of flight activity, and is called the buzz ratio (see Chapter 4 page 82).

Statistical analysis

Where appropriate, paired *t*-tests were used to compare upstream and downstream samples. Non-parametric Wilcoxon signed rank tests or sign tests were more commonly used, as most variables were not normally distributed. Spearman rank correlations were also used (Altman 1991). Where different tests were carried out using the same or closely related variables, the *P* values were adjusted using the Bonferroni method (Altman 1991). Adjusted *P* values are shown as *Pb*. Tests on counts of bat passes made by different species of bat were considered to be independent, and the *P* values were not adjusted. Statistical analyses were carried out on Systat release five for Windows (Wilkinson 1992), with a sample size of 19 unless indicated otherwise.

Results

Sewage treatment works

Spearman rank correlations were carried out to investigate the relationships between total bat passes, total terminal buzzes, and differences between upstream and downstream counts of these variables and the discharge river widths, dry flow rates, and dry flow rates / river widths of the sewage treatment works (Table 5.1). None of these relationships was significant ($Pb > 0.05$).

Time of sampling and distance from output

A Wilcoxon signed rank test was carried out to test numbers of bat passes recorded during all early samples against those recorded in all late samples, and no significant difference was found ($n = 38$; $Z = 1.064$). A Wilcoxon signed rank test of all distal sample points against all proximal sample points showed no significant difference in the numbers of bat passes recorded ($n = 38$; $Z = 1.222$). In Wilcoxon signed rank tests on numbers of terminal buzzes, no significant effects of early or late sampling ($n = 38$; $Z = 0.710$) or of distance to the output ($n = 38$; $Z = -0.998$) could be found. All P values were Bonferroni adjusted (Altman 1991).

In further analyses, numbers of bat passes and terminal buzzes recorded at individual sample points in a site were added together to form the upstream or downstream site count.

Bat activity and foraging effort upstream and downstream from sewage outputs

Total bat activity was higher upstream than downstream from 14 of the 19 sewage outputs. A paired t-test carried out on log transformed bat passes showed that bats were significantly more active in upstream sites than in downstream sites ($t = 2.553$; $P < 0.05$, Figure 5.1a). Compared to total upstream activity, downstream activity was reduced by 11%.

More terminal buzzes were counted upstream than downstream from 12 of the 19 sewage outputs. At three outputs, the opposite was true, at four, equal numbers of buzzes were counted upstream and downstream. A Wilcoxon signed rank test on total numbers of

terminal buzzes showed that bats were making significantly more attempts at prey capture per unit time at upstream sites than at downstream sites ($Z = -2.019$; $P < 0.05$, Figure 5.1b). Compared to total upstream buzz counts, downstream buzz counts were reduced by 28%.

Activity of bat species groups upstream and downstream from sewage outputs

All 5469 bat passes recorded were allocated to one of the five bat species groups. In total, 9.7% of bat passes were made by *Nyctalus* species or *Eptesicus serotinus*, 47.0% by *Myotis* species, and 43.3% by *Pipistrellus pipistrellus*. Of these, 36.5% were made by 45 kHz *Pipistrellus pipistrellus*, 62.6% by 55 kHz *Pipistrellus pipistrellus*, and 0.9% by unidentified *Pipistrellus pipistrellus*. The 22 bat passes making up this 0.9% were not included in further analyses.

Wilcoxon signed rank tests and sign tests were used to examine differences in bat pass numbers produced upstream and downstream from sewage outputs made by the following groups: *Nyctalus* species and *Eptesicus serotinus* ($Z = 0.553$; $P = 0.580$, no significant difference), *Myotis* species (sign test; $P = 1.00$, no significant difference), 45 kHz *Pipistrellus pipistrellus* ($Z = -3.073$; $P < 0.01$, more active upstream, Figure 5.2a), and 55 kHz *Pipistrellus pipistrellus* ($Z = -2.179$; $P < 0.05$, more active upstream, Figure 5.2b). Compared to total upstream activity, downstream activity of 45 kHz and 55 kHz *Pipistrellus pipistrellus* was reduced by 55% and 51% respectively.

Foraging effort of bat species groups upstream and downstream from sewage outputs

Terminal buzzes were produced by *Nyctalus* species and *Eptesicus serotinus* at only three sewage treatment works. Equal numbers of terminal buzzes were recorded at upstream and downstream sites in two cases.

Wilcoxon signed rank tests and sign tests were carried out on numbers of terminal buzzes produced at upstream and downstream sites by both 45 kHz and 55 kHz *Pipistrellus pipistrellus* and by *Myotis* species. Only 45 kHz *Pipistrellus pipistrellus* produced significantly higher numbers of terminal buzzes in upstream sites than in downstream sites (sign test; $Pb < 0.05$, Figure 5.3). Compared to total upstream buzz counts, downstream buzz counts were reduced by 87%. 55 kHz *Pipistrellus pipistrellus* produced similar numbers of buzzes at upstream and downstream sites (sign test, not significant), as did *Myotis* species. (Wilcoxon signed rank test, $Z = 1.897$, not significant). No significant

differences were found in buzz ratios produced by *Pipistrellus pipistrellus* upstream and downstream from outputs (Wilcoxon signed rank tests, $Z = -1.735$ for 45 kHz *Pipistrellus pipistrellus* and $Z = -0.712$ for 55 kHz *Pipistrellus pipistrellus; Pb* > 0.05).

Although *Myotis* species were equally active upstream and downstream from sewage outputs, they produced more terminal buzzes per unit time in downstream sites in nine cases, and more in upstream sites in three cases (this difference was not significant, as described above). For this species group, a further Wilcoxon signed rank test showed a significant difference in buzz ratios produced upstream and downstream from sewage outputs ($Z = 2.238$; $Pb < 0.05$, higher buzz ratio downstream, Figure 5.4). Compared to total upstream buzz ratios, downstream buzz ratios were increased by 112%.

Discussion

Bat activity and foraging effort upstream and downstream from sewage outputs

The total bat activity and the foraging effort per unit time were reduced downstream from sewage outputs (Figure 5.1). This indicates that river water quality is important in determining the quality of rivers as foraging sites for bats. No consistent trend could be found to explain the high degree of variation in the effect of different sewage outputs on bat activity. This variation could be due to a parameter which could not be quantified, such as the proximity of bat roosts (Kunz 1982).

Activity and foraging effort of bat species groups upstream and downstream from sewage outputs

Nyctalus species and *Eptesicus serotinus* produced similar numbers of bat passes and terminal buzzes upstream and downstream from sewage outputs. These large bats may not be dependent on water bodies as foraging sites. Although *Nyctalus noctula* does feed over rivers, it is not restricted to this foraging habitat (Gloor, Stutz & Ziswiler 1994-1995). Thus, populations of *Nyctalus* species and *Eptesicus serotinus* are unlikely to be affected by changes in river water quality. However, only 532 passes (9.7%) recorded in this study were made by this species group, and of these, 406 were recorded at Glastonbury sewage treatment works.

Most of the bat passes placed in the *Myotis* species group were probably made by *Myotis daubentonii*. This species is highly dependent on aquatic insects (Chapter 2), and occupies a distinct foraging niche. It often hunts over large water bodies, and takes prey from the water surface (Jones & Rayner 1988). The sibling species *Myotis brandtii* and *Myotis mystacinus* also hunt near inland waters, but their diets consist mainly of non-aquatic insects (Chapter 2). Although *Myotis* species were equally active upstream and downstream from sewage treatment works, they concentrated their feeding activity downstream (Figure 5.4), and may have been taking pollution-tolerant insects. Upstream sites may represent poor-quality foraging sites, but bats could be active there because of high levels of competition in downstream sites (see Bernstein, Krebs & Kacelnik 1991).

In mainland Europe, numbers of *Myotis daubentonii* have increased in several hibernacula (Červený & Bürger 1990; Weinreich & Oude Voshaar 1992; Harrje 1994), and this may be because of the eutrophication of inland fresh waters (Daan 1980; Kokurewicz 1994-1995). *Myotis* species, and especially *Myotis daubentonii*, may benefit from increasing availability of pollution-tolerant insects due to organic pollution and eutrophication.

The high numbers of bat passes recorded at sewage treatment works no. 1 (Box; Figure 5.1) may be explained by the presence of a *Myotis* maternity roost next to the downstream site. About 10 m from one downstream sample point was a stone railway bridge over the river, which seemed suitable as a *Myotis daubentonii* maternity roost. Of the bat passes recorded at this sample point, 81% were attributed to *Myotis* species. At all other sample points, 44% of passes were made by bats in this group.

The activity levels of 44 and 55 kHz *Pipistrellus pipistrellus* were reduced after the addition of treated sewage to rivers (Figure 5.2). 45 kHz *Pipistrellus pipistrellus* made more attempts at prey capture per unit time upstream than downstream from sewage outputs (Figure 5.3). This species may be more dependent on pollution-sensitive insects than 55 kHz *Pipistrellus pipistrellus*. However, attempts at prey capture by 45 kHz *Pipistrellus pipistrellus* per unit of flight activity were similar upstream and downstream from outputs. This suggests that, although upstream sites could support higher bat activity and perhaps more prey items than downstream sites, upstream and downstream sites were similar in terms of foraging habitat quality. Perhaps competition or interference from the high numbers of *Pipistrellus pipistrellus* active at upstream sites prevented bats from feeding at high rates there.

Although *Pipistrellus pipistrellus* is the commonest bat species in Great Britain, it has probably suffered large population declines over the past 30 years (data of R.E.

Stebbings in Harris *et al.* 1995). A deterioration of foraging conditions attributed partly to water pollution is thought to be the cause of the decline of a population in an industrialised area of Sweden. A rural population was found to be more stable, and consisted of individuals more likely to survive hibernation (Gerell & Lundberg 1993).

The effects of the discharge of treated sewage to rivers on bats might be restricted to the habitat immediately downstream from outputs. However, this study shows that river water quality may have consequences for bat foraging, and that these consequences may be different for different bat species. It is important to understand further the implications of possible changes in water quality for bat conservation.

Table 5.1 The 19 sewage treatment works in order of sampling. The dry flow rate is the output allowed by the National Rivers Authority per day in dry weather.

Works no.	Works name	Dry flow rate (m^3/day)	River (estimated width in meters)	OS grid reference of output
1	Box	580	By Brook (4)	ST 823 688
2	Melksham	5 000	South Brook (1)	ST 898 639
3	Chew Stoke	1 830	Chew (3)	ST 571 621
4	Saltford	25 740	Avon (25)	ST 691 689
5	Great Somerford	170	Avon (10)	ST 964 832
6	Lyneham	149	Strings Water (1)	SU 030 783
7	Freshford	460	Avon (15)	ST 790 606
8	Keynsham	4 720	Avon (30)	ST 666 693
9	Chippenham	10 000	Avon (7)	ST 918 711
10	Malmesbury	2 400	Avon (6)	ST 944 868
11	Bowerhill	1 650	Berryfield Stream (1)	ST 903 624
12	Paulton	1 600	Cam Brook (2)	ST 656 577
13	Thingley	3 750	Bydemill Brook (1)	ST 886 693
14	Wootton Bassett	2 300	Hancocks Water (1)	ST 073 814
15	Hilmarton	140	Cowage Brook (1)	ST 015 758
16	Sutton Benger	1 635	Avon (20)	ST 957 786
17	Keevil	795	Semington Brook (5)	ST 929 593
18	Glastonbury	5 200	Brue (5)	ST 486 383
19	Cheddar	2 968	Cheddar Yeo (5)	ST 447 524

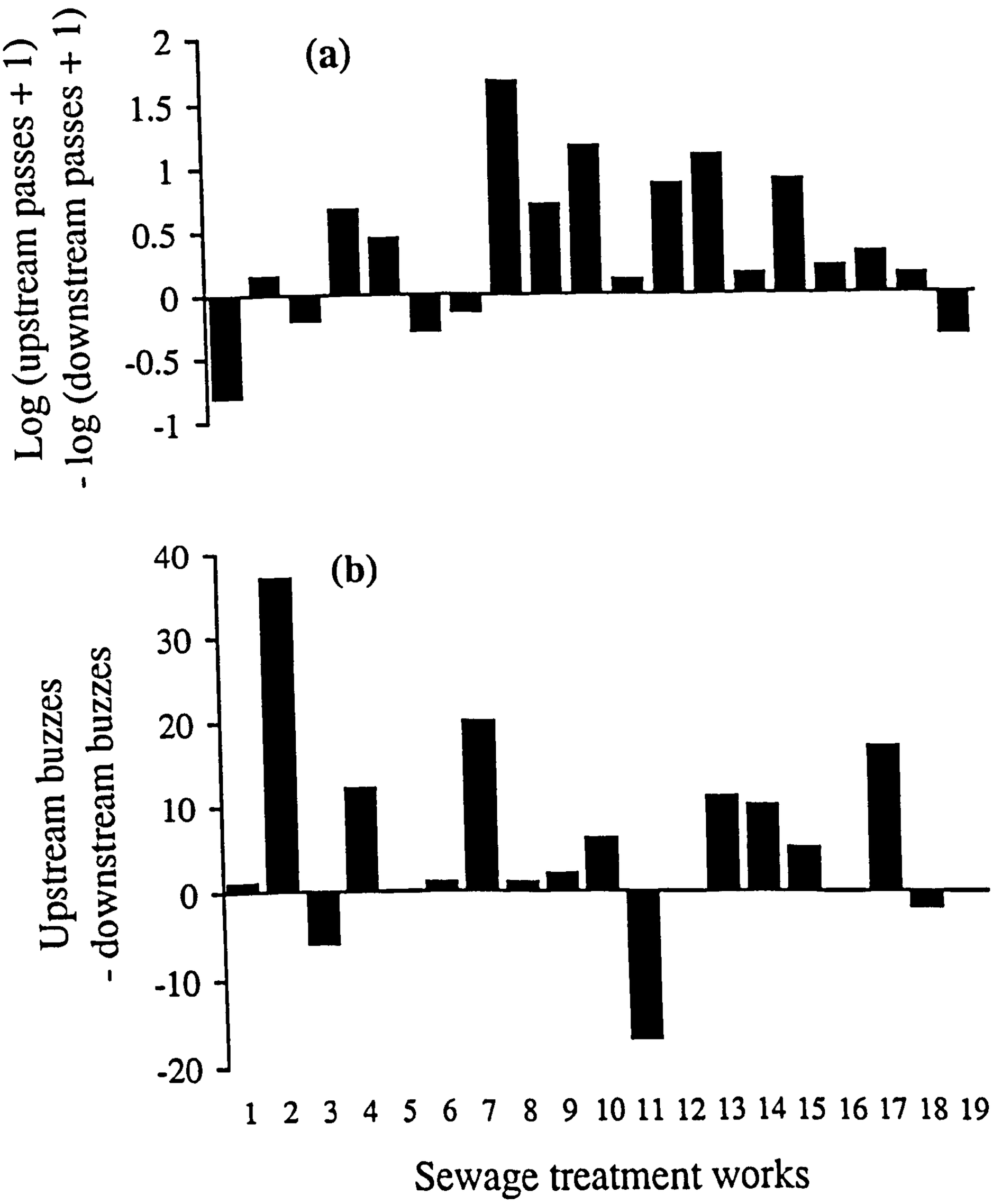


Figure 5.1 **(a)** The differences in log bat passes (upstream minus downstream) at the 19 sewage treatment works. A negative value indicates that bat activity was higher at the downstream site than at the upstream site. Bats were significantly more active upstream than downstream ($t = 2.553$; $P < 0.05$) and **(b)** the differences in terminal buzzes counted (upstream minus downstream) at the 19 sewage treatment works. Bats made significantly more attempts at prey capture at upstream sites than at downstream sites ($Z = -2.019$; $P < 0.05$).

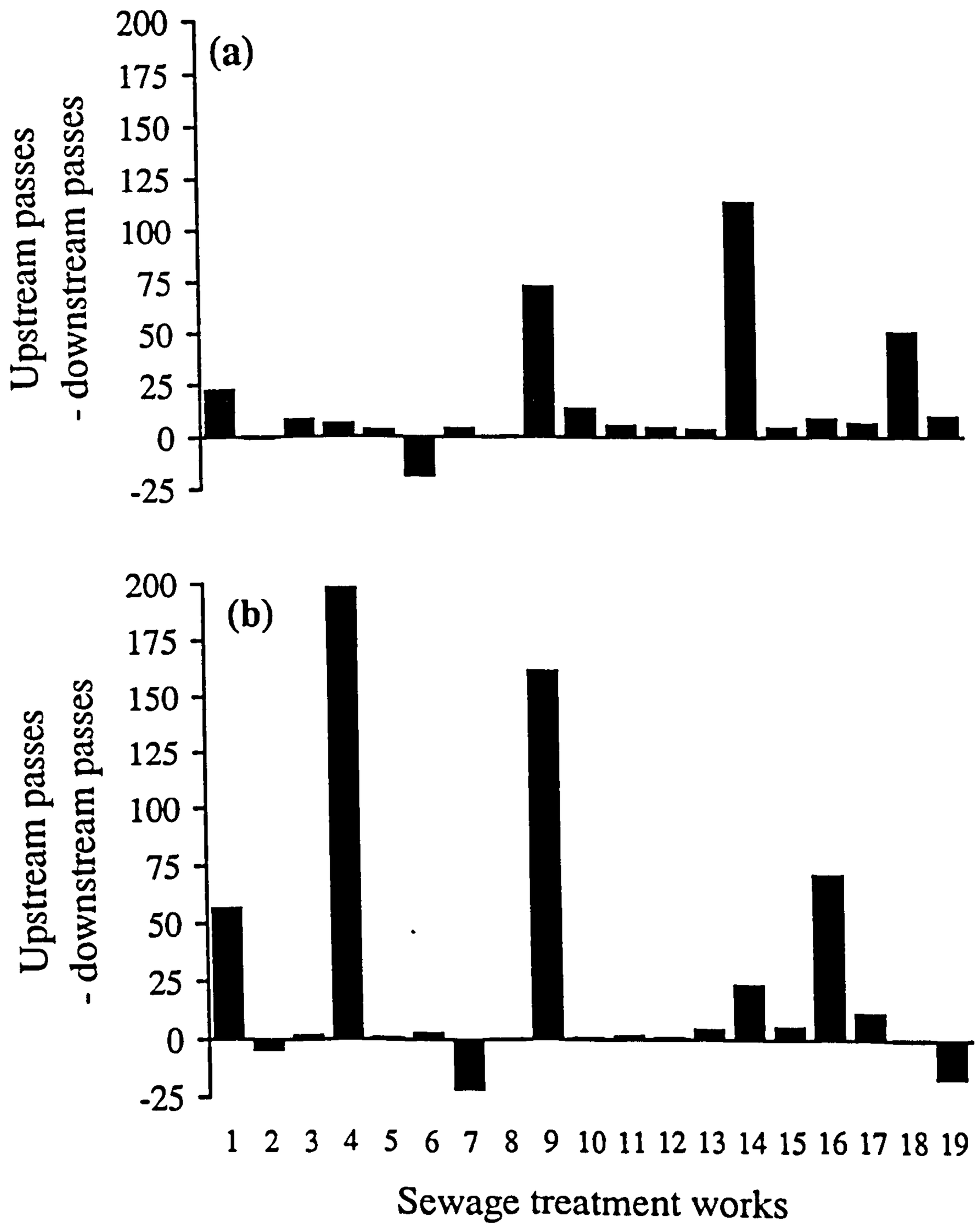


Figure 5.2 The differences between counts of passes made in upstream sites and in downstream sites by (**a**) 45 kHz *Pipistrellus pipistrellus* (significantly more active upstream than downstream, $Z = -3.073$; $P < 0.01$) and by (**b**) 55 kHz *Pipistrellus pipistrellus* (significantly more active upstream than downstream, $Z = -2.179$; $P < 0.05$). A negative value indicates that activity was higher at the downstream site than at the upstream site.

Figure 5.3 The differences in numbers of terminal buzzes made by 45 kHz *Pipistrellus pipistrellus* in upstream sites and in downstream sites. A negative value indicates that more terminal buzzes were made at the downstream site than at the upstream site. This species made significantly more attempts at prey capture in upstream sites than in downstream sites (sign test; $P < 0.05$).

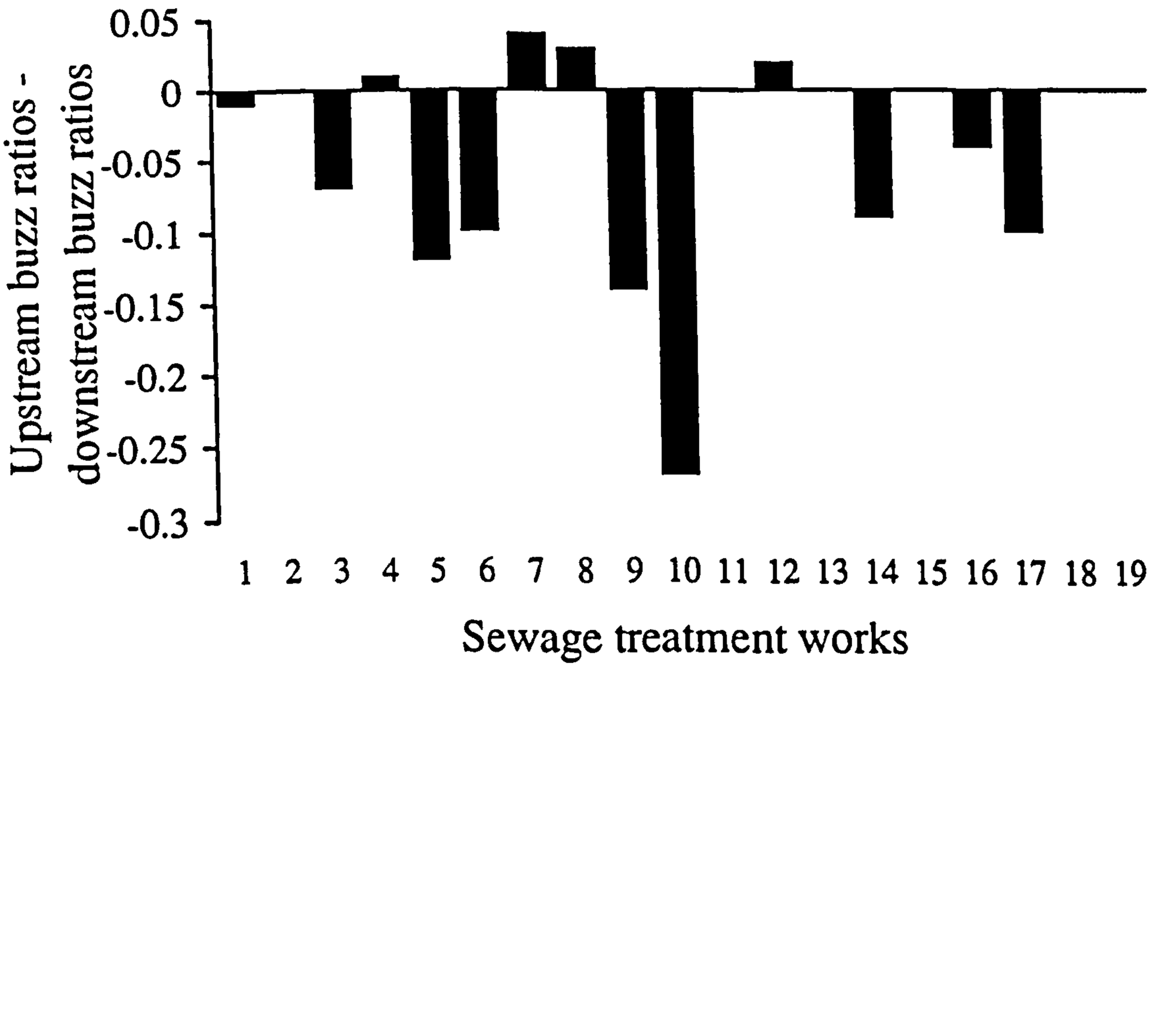


Figure 5.4 The differences in terminal buzz ratios in upstream and downstream sites made by *Myotis* species. A negative value indicates that the terminal buzz ratio was higher at the downstream site than at the upstream site. Significantly more attempts at prey capture per unit of flight activity were made in downstream sites than in upstream sites (Wilcoxon signed rank test, $Z = 2.238$; $Pb < 0.05$).

SIX

Conclusion

SIX

Conclusion

The bat community in Great Britain consists of 16 species, many of which occupy very similar ecological niches. There are however differences in all the aspects of the bats' ecology discussed in this thesis.

Differences in diet may be subtle and need further study, but the conservation of aquatic Diptera would benefit many species of bats (Chapter 2). Differences in the echolocation call structure of British bats make their identification at foraging sites possible from broad-band recordings of the calls. However, the *Myotis* species produce calls which are very similar in structure, and cannot be identified with complete certainty (Chapter 3). Differences in large-scale foraging habitat use show that rivers and lakes are used more by foraging bats than other habitats, but that pastures and woodlands may be important for some species (Chapter 4). On a small scale, changes in water quality are likely to affect different bat species in different ways. If the current decline in river water quality in England and Wales continues (Garland 1991; National Rivers Authority 1991), *Pipistrellus pipistrellus* may suffer population declines, while populations of *Myotis daubentonii* may benefit (Chapter 5). However, there is some evidence for a recent slight improvement in overall water quality (National Rivers Authority 1994).

In this concluding chapter, I sum up the information presented in this thesis, and what little is known about population trends of bats in Great Britain, for each bat species separately. I also give general recommendations for conservation measures and future research.

Rhinolophus ferrumequinum

There is strong evidence for the rapid decline of *Rhinolophus ferrumequinum* populations during the last hundred years (Ransome 1989; Harris *et al.* 1995). This species hunts mainly Coleoptera and Lepidoptera, by hawking and perch-hunting (Chapter 2). It uses FM/CF/FM echolocation calls which can be distinguished from those of other British bat

species unambiguously (Chapter 3). The most important habitats for *Rhinolophus ferrumequinum* appear to be pasture, where *Aphodius* dung beetles are taken, and woodland (Jones, Duvergé & Ransome 1995). Similar habitat preferences are described in this thesis, but very few passes made by this species were recorded (Chapter 4). As individuals of *Rhinolophus ferrumequinum* generally forage within 4 km of the roost (Jones, Duvergé & Ransome 1995), habitat management should perhaps be concentrated near known roosts. In the future, bat detector surveys or radio-telemetry should be used to locate as yet unknown roosts.

Rhinolophus hipposideros

Rhinolophus hipposideros uses FM/CF/FM echolocation calls which can be distinguished from those of other British bat species unambiguously (Chapter 3), and takes mainly swarming crepuscular Diptera by hawking (Chapter 2). These insects are commonly found in damp areas and near water. More work is needed to define the precise habitat needs of this species, and to clarify its population trends (Harris *et al.* 1995), but *Rhinolophus hipposideros* would probably benefit from the conservation of crepuscular Diptera.

Myotis brandtii

Little is known about the diet of *Myotis brandtii*, but it probably takes mainly families of Diptera found in damp woodland, by gleaning and hawking (Chapter 2). The FM echolocation calls used by this species can be distinguished from those of other *Myotis* and *Plecotus* species with around 70% certainty (Chapter 3). *Myotis brandtii* forages over rivers and lakes and in woodlands (Chapter 4). More work is needed on all aspects of the biology and population ecology of this species (Harris *et al.* 1995), but populations of *Myotis brandtii* would probably benefit from the conservation of woodland and aquatic Diptera.

Myotis mystacinus

Myotis mystacinus eats insects belonging to a wide range of families of Diptera, found in many habitats (Chapter 2). Calls of *Myotis mystacinus* are FM and can be distinguished from those of other *Myotis* and *Plecotus* species with around 70% certainty (Chapter 3). *Myotis mystacinus* forages over rivers and lakes, over grassland and in woodlands (Chapter 4), and its populations would probably benefit from conservation measures for aquatic and other Diptera. Like its sibling species *Myotis brandtii*, *Myotis mystacinus* is poorly-studied. A decline in numbers of *Myotis brandtii / mystacinus* has probably taken place in the last hundred years, although clear evidence is lacking (Harris *et al.* 1995).

Myotis bechsteinii

Very little is known about the rare *Myotis bechsteinii*, and much more research is necessary. Its diet suggests that this species inhabits woodlands and feeds by gleaning (Chapter 2). Echolocation calls produced by *Myotis bechsteinii* are broad-band FM sweeps, similar to those of other *Myotis* species (Chapter 3). The population trends of *Myotis bechsteinii* are unknown (Harris *et al.* 1995).

Myotis nattereri

Myotis nattereri produces very broad-band FM echolocation calls, which can be distinguished from those of other *Myotis* and *Plecotus* species with around 70% certainty (Chapter 3). It feeds mostly on diurnal Diptera, which it gleans from the surfaces of leaves (Chapter 2), and forages over rivers and lakes and in woodlands (Chapter 4). Conservation measures for *Myotis nattereri* should concentrate on diurnal Diptera; field research should focus on population ecology. The population trends of this species are unknown (Harris *et al.* 1995).

Myotis daubentonii

Myotis daubentonii hunts almost exclusively over rivers and lakes (Chapter 4), and feeds on aquatic Diptera (mostly Chironomidae) swarming above the water surface (Chapter 2). It uses FM echolocation calls, which can be distinguished from those of other *Myotis* and *Plecotus* species with around 70% certainty (Chapter 3). *Myotis daubentonii* may be able to benefit from eutrophication and other forms of pollution of inland waters (Chapter 5), as numbers of the pollution-tolerant Chironomidae are likely to increase if water quality decreases (Jeffries & Mills 1990). Populations of this bat species are probably not immediately threatened; although trends in Great Britain are unknown (Harris *et al.* 1995), numbers of hibernating *Myotis daubentonii* have increased in some parts of Europe in the last 40 years (Červený & Bürger 1990; Weinreich & Oude Voshaar 1992; Harrje 1994).

Pipistrellus nathusii

Very little is known about the status of *Pipistrellus nathusii* in Great Britain, but it seems to be more common than previously believed (Barlow & Jones 1996; see Chapter 4). It uses FM/CF echolocation calls, of lower peak frequency (around 39 kHz) than those of *Pipistrellus pipistrellus*, and distinguishable from other FM/CF calls with around 90% certainty (Chapter 3). *Pipistrellus nathusii* feeds mainly on aquatic Diptera (Chironomidae; Chapter 2), and the conservation of freshwater habitats may lead to population increases. However, as *Pipistrellus nathusii* is able, like *Myotis daubentonii*, to exploit Chironomidae, its populations might benefit from eutrophication. In Great Britain, virtually no field research on *Pipistrellus nathusii* has been carried out, and as yet, only one mating roost is known and no maternity roosts have been found (Barlow & Jones 1996).

45 kHz and 55 kHz *Pipistrellus pipistrellus*

The diet of *Pipistrellus pipistrellus* consists mainly of Diptera, many of which are aquatic (Chapter 2). The echolocation calls of both sibling species are distinguishable from each other and from other FM/CF calls with around 90% certainty (Chapter 3). Populations of

Pipistrellus pipistrellus are probably declining (data of R.E. Stebbings in Harris *et al.* 1995).

45 kHz *Pipistrellus pipistrellus* uses FM/CF echolocation calls with peak frequency at around 46 kHz (Chapter 3), and feeds in many habitats, especially over rivers and lakes and in woodland. The habitat use of this species is affected by temperature (Chapter 4). Over rivers with sewage works, 45 kHz *Pipistrellus pipistrellus* concentrates its foraging activity upstream from outputs, and it may feed on aquatic insects which are sensitive to pollution (Chapter 5). Therefore, water quality may be important in determining the quality of foraging habitats for this species.

55 kHz *Pipistrellus pipistrellus* uses FM/CF echolocation calls with peak frequency at around 54 kHz (Chapter 3), and feeds mainly over rivers and lakes. The feeding rate of this species varies among the ten land use types sampled in Chapter 4, and is highest over rivers and lakes (Chapter 4). Freshwater habitats should be conserved for the benefit of 55 kHz *Pipistrellus pipistrellus* (Chapter 5).

It is probable that 55 kHz *Pipistrellus pipistrellus* is more dependent on aquatic insects and inland waters than 45 kHz *Pipistrellus pipistrellus*, but more work needs to be done on the biology and population ecology of the two sibling species.

Nyctalus leisleri

The echolocation calls used by *Nyctalus leisleri* are distinguishable from other FM/CF calls with around 90% certainty (Chapter 3). This species forages primarily over lakes, rivers and pastures (Chapter 4), and eats mainly Diptera caught by hawking (Chapter 2). The population trends of *Nyctalus leisleri* are not known (Harris *et al.* 1995).

Nyctalus noctula

This species is a high-flying aerial insectivore (Norberg & Rayner 1987; Jones 1995), which eats mostly Diptera, and to a lesser extent Coleoptera and Lepidoptera (Chapter 2). The echolocation calls of *Nyctalus noctula* are distinguishable from other FM/CF calls with around 90% certainty (Chapter 3). It is found in many habitats, but lakes and pasture are preferred (Gloor, Stutz & Ziswiler 1994-1995; see Chapter 4). There is no information on population trends of *Nyctalus noctula* (Harris *et al.* 1995).

Eptesicus serotinus

The calls of *Eptesicus serotinus* are distinguishable from other FM/CF calls with around 90% certainty (Chapter 3). This species forages over lakes, pastures and rivers (Chapter 4), and eats mostly Coleoptera (Catto, Hutson & Racey 1994; see Chapter 2). There is little information on population trends of *Eptesicus serotinus* (Harris *et al.* 1995).

Barbastella barbastellus

The echolocation calls and habitat use of *Barbastella barbastellus* have not been described in detail (Chapter 3). This species feeds almost entirely on Lepidoptera (Chapter 2), and the conservation of this insect order is necessary for the survival of *Barbastella barbastellus*. There has been a decline in the number of records of this species in Great Britain after a peak in the 1950s and 1960s (Arnold 1993), and at the same time, a decline in numbers and ranges of many nocturnal Lepidoptera has occurred (Fry & Lonsdale 1991). Moth populations are greatly reduced by urbanisation and other forms of land development such as deforesation. After these changes in land use, the numbers of Lepidoptera increase again slowly, but species diversity remains extremely low (Taylor, French & Woiwod 1978). The effect of low prey diversity on bats is unknown.

Plecotus auritus

Plecotus auritus uses FM echolocation calls which can be distinguished from those of *Myotis* species with around 70% certainty (Chapter 3). The calls are of low intensity (Waters & Jones 1995), and consequently *Plecotus auritus* is difficult to survey with the acoustic methods described here (Chapter 3). Although under-represented, it was recorded in many land use types (Chapter 4). This species has probably declined significantly in recent decades (data of R.E. Stebbings in Harris *et al.* 1995). The food of *Plecotus auritus* is comparatively well-studied, and consists mostly of tympanate Lepidoptera (see under '*Barbastella barbastellus*' above).

Plecotus austriacus

Plecotus austriacus uses echolocation calls which are similar in structure to those of *Plecotus auritus* (Ahlén 1990), and also feeds mainly on Lepidoptera (Chapter 2; see also under '*Barbastella barbastellus*' above). Population trends of *Plecotus austriacus* are unknown (Harris *et al.* 1995), and the biology and population ecology of this species require study.

Recommendations for conservation and research

Populations of bats are likely to change if the resources which they use change, or if the area of foraging habitat available to them changes. If declines occur, recovery will almost certainly be very slow (Hill & Smith 1984; Findley 1993). In the absence of more detailed information on the dietary and habitat requirements of bats in Great Britain, conservation efforts should be directed towards improving freshwater habitats, woodlands and pasture for insects and bats. The conservation of Diptera and the habitats in which they breed is of particular importance. These measures will benefit a large proportion of the species of bats found in Great Britain.

In freshwater habitats, variety in physical features leads to plant and invertebrate community diversity (Sutherland & Hill 1995). Canalising rivers, increasing river flow, removing vegetation, infilling meanders and ponds, and removing trees should be avoided (Fry & Lonsdale 1991). Dredging, if necessary at all, should be kept to a minimum (Sutherland & Hill 1995). Urbanisation of river banks should be limited if possible (Jones & Clark 1987). Ponds and lakes should have sloping margins stocked with terrestrial and aquatic plants. The vegetation on river banks should not be cut, and land in neighbouring fields and in the catchment area should not produce large quantities of fertiliser or pesticide runoff. Changes in the pH, oxygen level, and temperature of fresh water are likely to lead to changes in the insect fauna. Freshwater fish, feeding on aquatic insects, can reduce the abundance of insects in rivers and lakes significantly (Fry & Lonsdale 1991). Work should be done to establish whether or not game fish compete with bats for food resources.

Woodlands are used as foraging habitats by many bat species, especially by 45 kHz *Pipistrellus pipistrellus* and by *Myotis* species, and probably by *Rhinolophus* and *Plecotus*

species (Chapter 4). In woodlands, glades and road edges with shrubs and grass are good habitats for insects, and deciduous trees support more species of insect than conifers (Fry & Lonsdale 1991). Groups of trees should be left to mature, particularly in conifer plantations, where trees are normally cut for timber as soon as their growth rate slows down. Many woodland species of Diptera and Coleoptera are associated with dead or decaying wood, or with very mature trees (Sutherland & Hill 1995).

In grasslands, hedgerows (Lewis 1969) and emergent trees are probably important habitats for Diptera and for foraging bats (Gaisler & Kolibáč 1992; Peng, Sutton & Fletcher 1992). Hedgerows may be used by bats as corridors for movement between habitats (Limpens & Kapteyn 1991; Walsh 1995). The importance of *Aphodius* dung beetles for bats foraging over grassland should be investigated. It is possible that only pastures are good foraging sites for the bats which feed over grassland (e.g. *Rhinolophus ferrumequinum* and *Eptesicus serotinus*).

For the very rare or endangered bat species (e.g. *Rhinolophus ferrumequinum*, *Barbastella barbastellus*, *Pipistrellus nathusii*, *Plecotus austriacus* and *Myotis bechsteinii*), it may be profitable to concentrate efforts on finding roosts, so that the areas around them can be surveyed in great detail and managed intensively for bats and insects. The broad-band acoustic method of identifying bats described in Chapter 3 may be of use, although species identity should be confirmed by capture at roost sites.

In future surveys of foraging habitat use by bats, insect availability should be sampled at the time of sampling for bats. The hypothesis that conserving insects will also help to protect bat populations from decline should be tested. Paired sampling should be used, as this is the most practical way to control for environmental parameters. The broad-band acoustic methods used in Chapters 4 and 5 are suitable for the assessment of foraging habitat use, and allow the objective identification of flying bats from their echolocation calls. These and other similar techniques should be developed and improved, and perhaps these quantifiable broad-band methods will eventually supersede the use of narrow-band bat detectors.

In the future, the field research described in Chapters 4 and 5 could be repeated for comparison with the results presented here. It may be possible to discover how consistent bats' habitat preferences are.

Land use in Great Britain has changed markedly in the past under the influence of human culture, and will surely change in the future. For example, between 1984 and 1990 in Great Britain, the length of hedgerows decreased by 23%, but there was an increase in urban land, woodlands, and semi-natural land use types. The total area covered by rivers

and lakes is decreasing slightly (Barr *et al.* 1993). In south-west England, between 1945 and 1990, rough grazing decreased in area by about 40%, while managed land and rural land each decreased by about 5%. At the same time, woodland and urban land have increased in area, to about 120% and 170% their areas in 1945, respectively (Sinclair 1993). Changes in vegetation and in bat populations are also predicted to occur due to global climatic change (Scheel, Vincent & Cameron 1996). Climate change is expected to lead to changes in the distribution of land classes in Great Britain (Whitby 1992).

If bats are to remain features of the wildlife of Great Britain, the effects of such land use change and climate change on bat populations should be evaluated directly in field experiments as well as predicted from the results of work such as that described in this thesis. The conservation of bats probably requires dedicated land management schemes. However, practical habitat management experience is rarely documented. Ideally, all management should take the form of controlled experiments and should be followed by detailed monitoring. Publication of results should follow as a matter of course (Sutherland & Hill 1995). For bat species, foraging activity, numbers in roosts and breeding success should be measured in areas of rapid land use change, in order to evaluate the effects of land use change for management. Only with the results of such experiments can we hope to make accurate predictions about what lies ahead for populations of bats in Great Britain.

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